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Algal response to climate change in subarctic lakes with special focus on toxic cyanobacteria

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Tiivistelmä - Referat – Abstract

Tutkimuksen tavoitteet. Aiemmat tutkimukset ovat osoittaneet viime aikaisen ilmaston lämpenemisen johtavan järvien syanobakteerivaltaisuuteen sekä haitallisten leväkukintojen lisääntymiseen. Voimakkaita kukintoja muodostavien sekä myrkkyä tuottavien syanobakteerien on ennustettu lisääntyvän tulevaisuudessa. Yli kaksi kertaa globaalia keskiarvoa nopeammin lämpenevien arktisten alueiden syanobakteeriyhteisöjen vasteita ympäristön muutokseen ei kuitenkaan vielä tunneta tarpeeksi hyvin. Täten onkin tärkeää tutkia, kuinka levä- ja syanobakteeriyhteisöt ovat kehittyneet teollistumisen jälkeen, jotta subarktisten levä- ja syanobakteeriyhteisöjen muutoksia voidaan ymmärtää sekä ennustaa tulevaisuuden muuttuvassa ympäristössä. Tämän tutkimuksen tavoitteena on lisätä tietoa ilmaston lämpenemisen sekä järvien ruskettumisen vaikutuksista subarktisten järvien leväyhteisöihin kiinnittäen erityistä huomiota syanobakteereihin ja -toksiineihin.

Aineisto ja metodit. Nykyisiä sekä historiallisia perustuottajaryhmien runsauksia tutkittiin niitä edustavien sedimentoituneiden leväpigmenttien avulla 23 subarktisella järvellä, jotka sijaitsivat pitkällä lämpötila- ja kasvillisuusvyöhykegradientilla. Ns. pinta-pohjamenetelmää käytettiin, jotta voitiin tutkia sekä viimeisen 150 vuoden aikana tapahtuneita leväyhteisöjen sisäisiä muutoksia että laajempia koko subarktisen alueen järvien leväyhteisöt kattavia trendejä. Pigmentti- ja ympäristödata analysoitiin yhdessä käyttäen monimuuttuja-analyyseja (pääkomponenttianalyysi (PCA) ja redundanttisuusanalyysi (RDA)) sekä muita tilastollisia analyyseja, jotta mahdollisia yleisiä muutostrendejä sekä syanobakteerien runsauteen voimakkaimmin vaikuttavia ympäristömuuttujia voitiin tutkia.

Tulokset ja johtopäätökset. Leväyhteisöt ovat muuttuneet viimeisen 150 vuoden aikana ja yleinen kasvaneen perustuotannon trendi on havaittavissa. Järvien ruskettumista esiintyy kuusi, mänty ja koivumetsä (SPB)-vyöhykkeellä. Nykyiset leväyhteisöt ovat pääasiallisesti piilevävaltaisia. Syanobakteerien suhteelliset runsaudet ovat vähentyneet koko tutkimusalueella. Karulla (Ba)- ja tunturikoivu (MBW)-vyöhykkeellä havaittiin pigmenttidatan perusteella benthisiksi arvioitujen syanobakteerien huomattavaa runsauden vähenemistä sekä pieniä planktisia picosyanobakteerirunsauksia. SPB-vyöhykkeellä havaittiin syanobakteerien runsastumista ilmaston lämpenemisen sekä ruskettumisen vaikutuksesta ja muutos vaikuttanee myös haitallisten planktisten lajien runsastumiseen. Merkittävimmät syanobakteerirunsauksiin vaikuttavat ympäristömuuttujat ovat kokonaisfosfori, lämpötila ja orgaanisen aineksen määrä. Tulokset korostavat välitöntä tarvetta hillitä ilmaston lämpenemistä, jotta arktisten ja subarktisten järviekosysteemien uniikit eliöyhteisöt sekä ominaisuudet voidaan säilyttää ja syanotoksiinien vaaralliset esiintymät välttää.

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Tiivistelmä - Referat – Abstract

Aims of this study. Previous studies have shown cyanobacterial dominance and harmful cyanobacterial blooms to increase due to recent climate warming. The increase of aggressively blooming species and toxin-producing strains of cyanobacteria has been predicted to further increase in the future. However, information on the response of cyanobacteria communities to environmental forcing in the Arctic region – which is experiencing warming at over twice the rate compared to the global average – has been insufficient. Thus, it is crucial to study how algal and cyanobacterial communities have developed after industrialization to better understand and predict future trends of subarctic algal communities as well as changes within cyanobacteria communities experiencing environmental forcing. This study aims to provide information on the effect of recent climate warming and lake browning on algal communities in subarctic lakes, with a special focus on cyanobacteria and cyanotoxins.

Materials and methods. Modern and historical primary producer group abundances of 23 subarctic lakes located on an ideal temperature and vegetation gradient were studied using sedimentary algal pigments as a proxy. The top-bottom method was used to study both changes within algal communities during the last ca. 150 years and the broader trends in algal communities of subarctic lakes. Pigment data was analyzed together with environmental data using ordination analyses (principal component analysis (PCA) and redundancy analysis (RDA)) as well as other statistical analyses in order to determine possible trends of change and to reveal the environmental variables that have the strongest impact on cyanobacterial abundance.

Results and conclusions. Algal communities have changed during the last ca. 150 years and show a general trend of increased primary production as well as lake browning in the spruce, pine and birch (SPB) vegetation zone. Siliceous algae generally dominate modern algal communities, and relative abundances of cyanobacteria have declined throughout the vegetation gradient. Within the Barren (Ba)- and mountain birch woodland (MBW) vegetation zones, cyanobacteria communities show a marked decline in the abundance of assumed benthic species based on pigment data, and low abundances of planktic picocyanobacteria. However, due to climate warming and lake browning, abundances of cyanobacteria have increased in several sites within the SPB vegetation zone and are suspected to indicate an increase of harmful planktic species. The most significant environmental variables controlling the abundance of cyanobacteria were total phosphorus, temperature and the amount of organic matter. The results highlight the urgent need to mitigate climate warming in order to preserve the unique biota and characteristics of Arctic and subarctic lake ecosystems, and to prevent the possible harmful increase of cyanotoxins in these sensitive ecosystems.

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Introduction

Life appeared on planet Earth nearly 4 billion years ago. Among one of the first and most important lifeforms were oceanic cyanobacteria (Smil, 2012). Oldest cyanobacterial fossils are estimated to be 3.5 billion years old (Schopf, 2012). Evolution of oxygen-dependent life today has its foundation in the past oxygen-producing cyanobacteria that enabled the Great Oxidation Event ~2450 Ma ago (Schopf, 2012). Nowadays cyanobacteria have become more known for harmful toxic blooms, despite constituting an important part of algal communities in less-disturbed systems (Paerl & Paul, 2012). The increase of cyanobacterial blooms has roots in human-induced eutrophication of waterbodies and climate warming (Paerl & Paul, 2012).

By using a novel approach combining knowledge on aquatic ecotoxicology with palaeolimnological methodology, this study aims to provide information on the effect of recent climate warming on algal communities in vulnerable subarctic lakes, with a special focus on cyanobacteria and their toxins.

Subarctic lake ecosystems

The Arctic can be defined in many ways, for example: the area north of the Arctic Circle, the area north of the 10 °C July isotherm, or the area north of the tree-line. The subarctic is often used to describe the transitional zone between the treeline and the boreal forest zone, but in Finland, where the tree-line is more oroarctic, the term subarctic is used to cover the whole of Finnish Lapland (Sorvari, 2001). Based on the Arctic Monitoring and Assessment Programme classification (AMAP, 1998), the study area can be classified as part of the Arctic in a global perspective and the predicted future changes concerning the Arctic can be assumed to impact the subarctic in similar ways. However, a distinction is made throughout this thesis as lake ecosystems in the high Arctic and subarctic are not always comparable.

Subarctic lake ecosystems largely mirror the surrounding terrestrial subarctic environment (Usher, 2005; Barry et al. 2013). Physical and chemical characteristics include seasonally limited solar radiation input, strong seasonal variation of temperature, permafrost, long icecover periods and limited amount of nutrients (Usher, 2005; Vincent et al. 2008A; Barry et al. 2013). Thus, the subarctic environment supports rather simple communities of organisms with a varying range of biotic complexity (Usher, 2005; Vincent et al. 2008A; Barry et al. 2013). The landscape with its geology, topography and vegetation also largely defines what kind of freshwater ecosystems are formed due to the shape of the basin, size- and environmental characteristics of the catchment area as well as the water volume (Wrona et al. 2006; Barry et al. 2013).

Solar radiation at high latitudes fluctuates from no light during the winter to light throughout the days and nights in the summer, resulting in large seasonal fluctuations in lake temperatures and light environment. The break-up and freeze-up dates of high latitude lakes are mostly determined by climate, water volume and snow cover (Vincent et al. 2008B). Precipitation in the subarctic is mostly snow and generally low thus the main influx of carbon and nutrients in subarctic lakes occurs during spring melt of snow and ice (Lyons & Finlay, 2008; Barry et al. 2013). Weathering is often limited due permafrost and cold temperatures (Lyons & Finlay, 2008).

Subarctic lake-ecosystems tend to be oligotrophic (low amount of nutrients) systems with low biodiversity and a short growing season (Usher et al. 2005; Lyons & Finlay, 2008; Barry et al. 2013). Thus, these lakes have a relatively low rate of planktic production and biomass (Lyons & Finlay, 2008). Benthic algae mostly dominate primary production, and as such, the production can also be limited by light availability (Lyons & Finlay, 2008; Quesada et al. 2008). Phosphorus is the limiting nutrient in subarctic lake ecosystems (Lyons & Finlay, 2008). The sediments are often oxic and have high capacity to bind phosphate (Lyons & Finlay, 2008). The benthic microbial mats can use the sediment-bound phosphorus due to sediment-degrading microbes in the mat communities (Quesada et al. 2008; Quiblier et al. 2013). Microbial loops degrade organism-produced carbon making it available for phytoplankton that in turn are predated by protozoans or metazoan bacterivores (Christoffersen et al. 2008). Dissolved organic carbon (DOC) is often the dominating form of carbon in these lakes. It is known to be sensitive to environmental changes, to reduce light availability, and to transport nutrients and trace elements (Lyons & Finlay, 2008). In subarctic lakes, DOC is mostly of terrestrial origin, though there is spatial variation in the composition and concentrations of DOC (Lyons & Finlay, 2008). The highest influx of DOC takes place most often during the spring melt and the mobilization of labile materials can lead to quick breakdown of substances and cycling of nutrients (Lyons & Finlay, 2008). Nitrogen in these ecosystems occurs mainly as dissolved organic nitrogen, the circulation of which is often coupled with DOC (Lyons & Finlay, 2008).

Food webs are simpler in subarctic lake ecosystems than in temperate environments, but they may present a range of biological complexity (Usher et al. 2005; Christoffersen et al. 2008). Subarctic lake food webs spread from simple microbial-loop communities to similar aquatic communities as in temperate regions including fish, macrophytes, insects and crustaceans (Christoffersen et al. 2008). The structure, functionality and metabolism of the microbial loop is based on influxes from the catchment area (Christoffersen et al. 2008). The primary producers consists of diatoms, dinoflagellates, chrysophytes and cyanobacteria (Christoffersen et al. 2008). They are grazed by copepods, cladocerans and rotifers, which in turn are predated by larger invertebrates or fish (Christoffersen et al. 2008).

Climate Change in the subarctic

Annual average surface air temperature in the Arctic has risen 2.7 °C from 1971 to 2017 with a rise during the cold season of 3.1 °C and 1.8 °C during the warm season (ACS, 2019). Warming in the Arctic has been predicted to continue by over twice the rate of the annual global average warming (ACS, 2019). In Finland, the annual mean temperature has increased by 0.93 ± 0.72 °C between 1909 and 2008, with the highest temperature rise in the spring (Tietäväinen et al. 2010). Moreover, these authors showed that winter temperature rise has increased during the last 50 years (3.47 ± 2.78 °C), and especially during the last 30 years (4.28 ± 3.44 °C).

Climate warming has been predicted to have severe global impacts. Lenton et al. (2019) suggest that evidence of high impact irreversible changes in biophysical systems is increasing. They consider the current situation a climate emergency and suggest that according to the IPCC 2018 report multiple tipping points will be exceeded even with 1-2 °C global warming. Several cryosphere tipping points are on the verge of being crossed, including Arctic sea ice, glaciers and the Greenland ice sheet (Steffen et al. 2018). Loss or severe decline of the cryosphere would have dramatic impacts globally by raising the sea level and directly on Arctic ecosystems for they are a crucial part in the formation of Arctic weather and climate (Steffen et al. 2018). Steffen et al. (2018) suggest that a global tipping point will be achieved with a ca. 2 °C warming.

Several climate change-driven predicted and observed changes in subarctic lake ecosystems have been observed. These include e.g. changes in stratification length, strength and depth (Sorvari et al. 2002; Edlund et al. 2017); changes in timing and length of ice-cover period (Smol et al. 2005; Weckström et al.2014); changes in temporal mixing dynamics (Vincent et al. 2011); increase in incoming nutrient and organic carbon fluxes (Vincent et al. 2011; Wrona et al. 2016; Finer et al. 2020); and changes in algal community structures (Flanagan et al. 2003; Edlund et al. 2017; Przytulska et al. 2017). The combined effects of all these changes might lead to a significant change in northern lake ecosystems.

Edlund et al. (2017) described a common trend for all their study lakes to be warming of summer surface water and for deeper lakes increased duration and frequency of temperature-based stratification. The responding changes in algal communities highlighted the difference of change between shallow and deeper lakes: in shallow lakes temperature, mixing, pH and habitat influenced diatom communities; in deeper lakes the communities were affected by thermocline depth, stability, and the indirect effects of previous factors to nutrient cycling and spring mixing (Edlund et al. 2017). Similar conclusions regarding differentiating responses to rising temperatures and nutrient concentrations have also been drawn in modelled cyanobacteria abundances in dimictic and polymictic lakes (Taranu et al. 2012). Flanagan et al. (2003) predict that primary production will grow dramatically in Arctic lakes if the predictions of rises in

temperature and nutrient concentrations are accurate. Przytulska et al. (2017) propose that occurrence of cyanobacterial blooms will increase in the Arctic in the future due to higher temperature, increased light availability (less snow on ice, shorter ice-cover periods) and change in nutrient fluxes. Microbial community trends towards diatom- and cyanobacteria-dominating communities have already been observed in shallow subarctic ponds (Teittinen et al. 2017), and abundance of cyanobacteria in subarctic lakes has increased during the last 200 years (Taranu et al. 2015). The increase in cyanobacterial abundance has also led to an increase of harmful species, which has been globally observed in many studies (e.g. Paerl & Paul, 2012; Rigosi et al. 2014; Taranu et al. 2015; Mantzouki et al. 2016; Pick 2016).

Greening and browning in the subarctic

Warming in the Arctic also enhances Arctic greening, which is described as increasing vegetation and productivity (Pearson et al. 2013). Greening is based on a longer growing season (Jeong et al. 2011), habitat migration (Sturm et al. 2001) and increased photosynthetic activity (Xu et al. 2013). Pearson et al. (2013) observed significant changes in composition, density and distribution of vegetation in the Arctic during the recent decades. They predict a marked increase of woody cover and vegetation class shifts in the future based on 2050's climate predictions. Pearson et al. (2013) also suggest that vegetation change overall will act as a positive feedback to climate.

Another phenomenon interacting with climate warming and Arctic greening is lake browning, which is a change in water color due to increased amounts of organic carbon entering aquatic ecosystems. In the Arctic, increased mobilization of DOC and colored dissolved organic matter (CDOM) is associated with higher temperature, precipitation and increased permafrost thaw (Wrona et al. 2016). Some lakes are by nature more colored due to mires and forest located in their catchments, but anthropogenic land use-induced increased leaching and transport of organic matter to water bodies can greatly further impact the water color of lakes and concentration of DOC (Klöve et al. 2012; Finer et al. 2020). Microbial degradation leads to degraded, smaller, mostly dissolved carbon substances, which are then transported via runoff ending up in the receiving water body (Klöve et al. 2012). CDOM has a high influence on the optical conditions of Arctic aquatic systems. Thus, it also has an impact on the distribution of the relative benthic and water column productivity (Wrona et al. 2016). In addition, these organic carbon substances are tightly bound with the circulation of nutrients, especially nitrogen (Finer et al. 2020).

Further lake browning is predicted in the Northern Hemisphere (de Wit et al. 2016). Increased permafrost thawing, weathering, soil/sediment erosion and thus increased DOC and nutrient load due to climate

warming and increased precipitation is estimated to either cause greening or browning of aquatic ecosystems in the Arctic depending on the magnitude of loading (Wrona et al. 2016).

Cyanobacteria

Cyanobacteria are photosynthetic prokaryotes, which all synthesize chlorophyll *a* (Whitton & Potts, 2012). The common name blue-green algae is derived from the pigment phycocyanin produced by most cyanobacteria, which makes cyanobacteria cells appear bluish when present in large amounts (Whitton & Potts, 2012). Benthic cyanobacteria most often form microbial mats that host a great diversity of microbes and other algae (Lizotte, 2008; Quesada et al. 2008; Kleinteich et al. 2012; Vincent & Quesada, 2012). Cyanobacteria create blooms (rapid increase of cells) caused by a favorable change in their environment (Whitton & Potts, 2012). Blooms of filamentous planktic cyanobacteria, however, are formed slowly over the growing season by mass accumulation (Vincent & Quesada, 2012). Knowledge on benthic cyanobacterial blooms is rather sparse and many key functions are still largely unknown (Quiblier et al. 2013).

Ecology of subarctic cyanobacteria

Studies concerning cyanobacterial species composition in the Arctic are rare (e.g. Lizotte, 2008; Jungblut et al. 2010). Completely new species and species previously not known to inhabit these areas have recently been found in many studies and it appears that similar species have evolved in both Arctic and Antarctic environments (Lizotte, 2008; Jungblut et al. 2010). Success of cyanobacteria in these harsh environments can be explained by adaptations and high tolerance of long cold periods, freeze-thaw cycles, changing light conditions, UV-radiation and drought (Vincent & Quesada, 2012). As elsewhere, cyanobacteria are spread throughout the lake ecosystems in the Arctic – they occur as planktic and benthic, (epiphytic and metaphytic) species (Lizotte, 2008). Cyanobacteria genera found in the subarctic are shown in Table 1. Most cyanobacteria-rich habitats are determined by the lakes' environmental properties -. For example in shallow clear water lakes most common species are benthic and in deeper lakes the abundance of planktic and benthic species is more even (Lizotte, 2008; Vincent & Quesada, 2012). In the Arctic, benthic cyanobacteria are present at great abundances and their dominance tends to increase in algal communities with increasing latitude (Sheath et al. 1996; Vincent & Quesada, 2012). Most abundant and diverse orders in Arctic lakes have been found to be Croococcales and Oscillatoriales. Croococcales inhabit lakes mostly as colonies or coccoid cells (Lizotte, 2008). They vary from benthic to planktic species. In the Arctic,

Oscillatoriales are mostly filamentous species without heterocysts and hence include mostly benthic genera (Lizotte, 2008). This order includes the bloom-forming species *Oscillatoria* and *Phormidium* (Lizotte, 2008).

Table 1. Cyanobacteria genera identified in the subarctic (Lizotte, 2008; Jungblut et al. 2010; Vincent & Quesada, 2012).

Order	**Genus**
Chroococcales	*Aphanocapsa* *Aphanothece* *Croococcus* *Gloeocapsa* *Microcystis* *Synechococcus* *Woronichinia*
Nostocales	*Anabaena* *Nostoc*
Oscillatoriales	*Oscillatoria* *Microcoleus* *Phormidium* *Plaktothrix*
Synechococcales	*Leptolyngbya*

Vincent & Quesada (2012) split polar cyanobacteria in three functional groups: picocyanobacteria, bloom-formers and mat-formers. Picocyanobacteria are abundant in and characteristic of oligotrophic high latitude lakes due to their high surface to volume- ratio (Vincent & Quesada, 2012). The most common genus of picocyanobacteria is *Synechococcus* (Lizotte et al. 2008; Vincent & Quesada, 2012). Species in this genus form a large amount of planktic biomass in many polar lakes, especially when phosphorus concentrations increase (Lizotte, 2008; Vincent & Quesada, 2012). Bloom-formers, such as *Anabaena*, *Microcystis* or *Aphanizomenon*, are largely absent in the high Arctic even in cases where nutrient levels have risen significantly (Vincent & Quesada, 2012). This suggests that the regulating factor for bloom-formers in the high Arctic is most likely temperature (Vincent & Quesada, 2012). Subarctic planktic colonies are mostly formed by *Anabaena* or/and *Microcystis* (Lizotte, 2008). Further invasions of new bloom-formers may occur in the future, if the Arctic continues to warm and nutrient input from the catchments will increase.

Mat-forming cyanobacteria are the most abundant functional group in the Arctic. These species form mats, films and aggregates on the lake sediment surface, rocks and aquatic mosses (Vincent & Quesada, 2012). Most typical benthic mat types in Arctic freshwaters have been identified as 1) black or brown colored

crusts covering shallow rocky areas typically dominated by *Gloeocapsa*, 2) black, yellow or green sheets of N_2-fixing *Nostoc* communities, 3) loose spherical *Nostoc* communities, and 4) benthic films and mats formed by filamentous Oscillariales, in which *Leptolyngbya*, *Phormidium*, *Microcoleus* and *Oscillatoria* are the most common genera. Microbial mats are multilayered trophically and biogeochemically interdependent microbial assemblages, in which cyanobacteria are the dominating biota (Quesada et al. 2008; Vincent & Quesada, 2012). Filamentous cyanobacteria form the sponge-like structure of the mat. The surface of the mat is often dominated by species capable of quenching highly toxic reactive oxygen species produced by UVR exposure (Quesada et al. 2008), thus the surface layer usually contains high concentrations of photoprotective pigments (Bonilla et al. 2005; Vincent & Quesada, 2012). Deeper layers contain highest mass of active cyanobacteria, chlorophytes and diatoms and thus hold higher concentrations of light capturing pigments (Bonilla et al. 2005; Vincent & Quesada, 2012). Deepest layers of the mat contain a variety of bacteria and viruses enabling efficient recycling, sedimentary uptake and mineralization of nutrients (Vincent & Quesada, 2012). The small holes and tunnels inside the mat structure provide channels for nutrient transfer, act as microhabitats for smaller-celled organisms, and allow movement for filamentous cyanobacteria and grazers (Quesada et al. 2008; Vincent & Quesada; 2012). Due to the nutrient scavenging and regeneration mats contain higher concentrations of soluble reactive phosphorus and ammonium than the water column above (Vincent & Quesada, 2012). The producers in the mats support communities of grazers like rotifers, nematodes and chironomid larvae (Bonilla et al. 2005; Vincent & Quesada, 2012).

Growth limiting factors of benthic cyanobacterial mats are not yet fully understood. As the communities are efficient in nutrient recycling and uptake, they are not so dependent on nutrient concentrations of the water column. As shown by Bonilla et al. (2005), no increase in benthic mat growth was observed with nutrient enrichment over eight days when phytoplankton reacted by multiplying several fold. It is, however, possible a longer period of nutrient enrichment could increase benthic biomass as well. Vincent & Quesada (2012) propose that physical factors like scouring, gas accumulation, drying and erosion might be the most effective controllers of mat biomass. Grazing by invertebrates and protozoans is unlikely to be a significant controlling mechanism due to slow growth and short growing season of grazers (Bonilla et al. 2005). Temperature inhibition of bacterial degradation might explain mat growth via slow mineralization rates (Vincent & Quesada, 2012).

Sheath et al. (1996) found a general trend of increasing relative abundance of cyanobacteria from low to high Arctic. Despite their adaptive capability and dominance of many Arctic freshwaters, cyanobacteria do not always dominate algal communities of Arctic and subarctic lakes. The Arctic is a mosaic of different environments. Pavlova et al. (2016) found that the proportion of cyanobacteria in Western Siberia

thermokarst lakes never exceeded 20 %, probably due to the acidic nature of these water bodies. However, in eutrophic Russian tundra lakes with neutral water pH, cyanobacteria dominated the algal communities with relative abundances over 75 % (Trifonova, 1998). Acidity and coloration of the water might thus strongly control the structure of cyanobacterial communities.

Harmful species

Identification of toxin producing cyanobacteria species and strains is still globally an ongoing process. Widely distributed toxin-producing genera have been identified as 1) planktic nitrogen fixing *Anabaena, Aphanizomenon, Cylindrospermopsis*, *Nodularia*, 2) non-nitrogen fixing *Microcystis* and *Planktothrix*, 3) benthic nitrogen fixing *Lyngbya*, *Hormothamnion* and *Oscillatoria*, and 4) non-nitrogen fixing *Phormidium*, *Symploca* and *Oscillatoria* (Paerl & Paul, 2012). Due to the development in DNA- and RNA-identification technology, an increasing number of harmful species can be identified (Kleinteich et al. 2012). Benthic species are underrepresented as studies on harmful planktic blooms are more common (Kleinteich et al. 2012). The controlling mechanisms of toxin production and out of cell excretion are still largely unknown. The purpose of toxin production is also unclear. The most common theory is the protection from grazing (DeMott & Moxter, 1991). However, Rantala et al. (2004) have estimated that the cyanobacterial toxin production capability could be up to 2000 million years old, thus possibly older than the earliest eukaryote crown lineages. They suggest that the purpose of microcystin production might lie in scavenging trace metals or in signaling and gene regulation.

Cyanotoxins and their toxicity

Cyanotoxins are a chemically variable group of cyanobacterial metabolites, and they are usually categorized by the primary target of toxicity. Microcystins (MC), nodularin and cylindrospermopsin (CYN) are known hepatotoxins targeting liver (Sivonen & Jones, 1999). Anatoxin-a (Homo- & -A(TX)) and saxitoxins (STX) are known neurotoxins targeting neurons (Sivonen & Jones, 1999). Cyanotoxins are proven to be very harmful to many organisms and several cases of animal poisoning and death have been reported (Sivonen & Jones, 1999; Quiblier et al. 2013). Microcystin variants have been found in several studies of cyanobacterial mats in Arctic lakes (Kleinteich et al. 2013; Trout-Hailey et al. 2016; Kleinteich et al. 2018). Saxitoxin has been so far found in only one study (Kleinteich et al. 2013).

Microcystins are the largest group of cyanotoxins with 60 chemical variants (Kaebernick & Neilan, 2001). They are mainly recognized as hepatotoxins that inhibit eukaryotic protein phosphatases and thus result in phosphorylation of cytoskeletal laments, which eventually will lead to liver failure (Kaebernick & Neilan, 2001).

There are many studies describing the toxicity of cyanotoxins to different organisms, from water flees (*Daphnia* sp.) to humans, and cyanotoxins have been found to be a threat to water safety (eg. Paerl & Paul, 2012; Quiblier et al. 2013; Drobac et al. 2016). However, only few extensive studies focusing on the lethal toxicity to aquatic organisms have been conducted (DeMott et al. 1991; Kotak et al. 1996)(Table 2). Some studies indicate that aquatic organisms show higher tolerance to cyanotoxins (Ibelings & Havens, 2008). Microcystins, nodularin, anatoxin-a and saxitoxin are classified as extremely toxic, and cylindrospermopsin as highly toxic on the toxicity classification scale by Hodge & Sterner (2005). More toxicity data of cyanotoxins is needed in order to form a more comprehensive understanding of their role in the environment in the future.

Table 2. Toxicity values of different cyanotoxins.

Toxin	**Studied lethal dose 50% (LD50) or lethal concentration 50% (LC50)**	
Microcystins	LD50 MC-LR Rainbow trout (*Oncorhynchus mykiss*) ~500 μg^{-1} kg LD50 Mice MC-LR 43 μg^{-1} kg bw Mice MC-RR 235.4 μg^{-1} kg bw Mice MC-YR 110.6 μg^{-1} kg bw	Kotak et al. 1996 Gupta et al. 2003
Nodularin	*Daphnia* LC50 *D. pulicaria* 14.1 (48 h) μg^{-1} ml *D. hyalina* 3.9 (48 h) μg^{-1} ml *D. birgel* (single) 0.57 (24 h), 0.52 (48 h) μg^{-1} ml IC50 *E. Coli* 5.6 ng^{-1} ml	DeMott et al. 1991 Liu et al. 2005
Cylindrospermopsin	LD50 Mice 10 mg^{-1} kg (10 000 μg^{-1} kg)	Banker et al. 2001
Anatoxin-a	LD50 Mice 200 μg^{-1} kg	Carmichael, 1997
Saxitoxin	LD50 Mice 5d 10 μg^{-1} kg bw	Halstead et al. 1984

Behavior and fate in the environment

Bioaccumulation of microcystin in organisms has been observed on all trophic levels (e.g. zebrafish (Wu et al. 2016), crayfish (*Procambarus clarkii*) (Rios et al. 2013), and mussels (Halstead et al. 1984)), whereas

biomagnification is not (Ibelings & Havens 2008). Rather than biomagnification *per se*, changes can be seen as biodilution via excretion, degradation and metabolic defense mechanisms (Ibelings & Havens 2008). The danger of bioaccumulation in crayfish and mussels is that these organisms do not degrade the toxins in their system (Halstead et al. 1984; Rios et al. 2013), but store them in their tissues, thus creating a potential risk of poisoning for organisms and people eating them (Rios et al. 2013).

The chemical fate of cyanotoxins is also rather unclear. According to Quiblier et al. (2013), it appears that photodegradation of cyanotoxins is one major degradation pathway. Photodegradation by UV-radiation is still rather slow – for MCs from 2-6 weeks (Quiblier et al. 2013). Biological degradation is also suggested to be one of the main degradation pathways and some microbes have been found to degrade cyanotoxins in the water column and in the sediment (Quiblier et al. 2013). Sorption to particles can also be one further major pathway of removal from the water column. Sediments with high clay and/or organic matter content are proven to be efficient in binding cyanotoxins (Klitzke et al. 2011). According to Sivonen & Jones (1999), cyanotoxins can persists in natural conditions from several months to several years.

This study

Palaeolimnology is the key approach for studying the past - by knowing how the environment has responded to changes in the past it is possible to predict the future (Smol, 1992). As usually no monitoring data exists beyond the recent decades, indirect environmental indicators (proxy data) are the only way to provide information from time periods preceding instrumental data sets (Smol, 1992). Proxies are a wide group of physical, biotic, geochemical or molecular indicators that record environmental change (Smol, 1992). The history of lakes and their surroundings is stored in the sediment layers of lakes. Developments in dating methods have made it possible to place the observed changes in a timeline (Smol, 1992). In addition to using multiple proxies reacting to one disturbance (e.g. pH) or to different disturbances (e.g. pH, ice-cover period), combining the proxy-based information with monitoring data and/or other biological, chemical or geological information can be tremendously valuable (Smol, 1992; Smol & Cumming, 2000).

Ecotoxicology is focused on the environmental impact of human-induced release of various chemicals into the environment regardless if the chemicals are natural or synthetic by nature (Lynch et al. 2001). Impacts of a chemical on biota ranging from plants to people are always tied with the amount of chemical released, bioavailability, dose to individual - population, mechanisms of uptake, chemical characteristics, and physico-chemical characteristics of the environment (Lynch et al. 2001).

Analyzing plant pigments stored in lake sediments provides information of pigment producers: algae, cyanobacteria and higher plants (McGowan et al. 2005). Pigment producers have specific pigment signatures that can be used to separate genera and functional groups (McGowan et al. 2005). Fossil pigments have been used as a proxy to study algal communities of lakes (Smol & Cumming, 2000), UV penetration (Leavitt et al. 1997), and as pigment ratios to determine past ice cover and climate (Lami et al. 1998). Pigments can be used as indicators of past primary production and primary-producer community composition. This information can further be used to estimate the past trophic history of lakes.

The general aim of this study is to provide a better understanding on the development of subarctic algal communities, especially cyanobacteria, after the 1850's industrialization, and to recognize possible shifts in their community structures in order to better predict possible future trends. Additional goals are to recognize the environmental variables with the strongest impact on the algal community structures, and to use the gained information for further studies relating to cyanobacterial communities and toxin production in the subarctic region.

The hypotheses of the study are

1. The modern structure of algal communities is based on diatom- and cyanobacteria-controlled systems in the research area (Teittinen et al. 2017)
2. In lakes that have experienced browning benthic species abundance has declined due to lower light availability (Vadeboncoeur et al. 2003; Wrona et al. 2016), whereas planktic cyanobacteria have increased due to browning in lakes with optimal DOC (~7 mg l^{-1}) (Feuchtmayr et al. 2019) and water color (10 to 20 Pt l^{-1}) (Carvalho et al. 2011)
3. Toxin-producing groups have increased (Flanagan et al. 2003; Przytulska et al. 2017)
4. Environmental variables with strongest impact on the cyanobacteria communities are light and nutrient availability coupled with temperature (Vadeboncoeur et al. 2003; Karlsson et al. 2005; Elliott, 2012; Wrona et al. 2016).

The main research questions are

1. Have the relative group abundances of subarctic algal communities changed during the last ca. 150 years?
2. Have subarctic cyanobacterial communities changed during the last ca. 150 years?
3. Which environmental variables are mainly controlling the distribution and structure of cyanobacterial communities?
4. How will the predicted climate warming and brownification affect cyanobacterial communities?

Material & methods

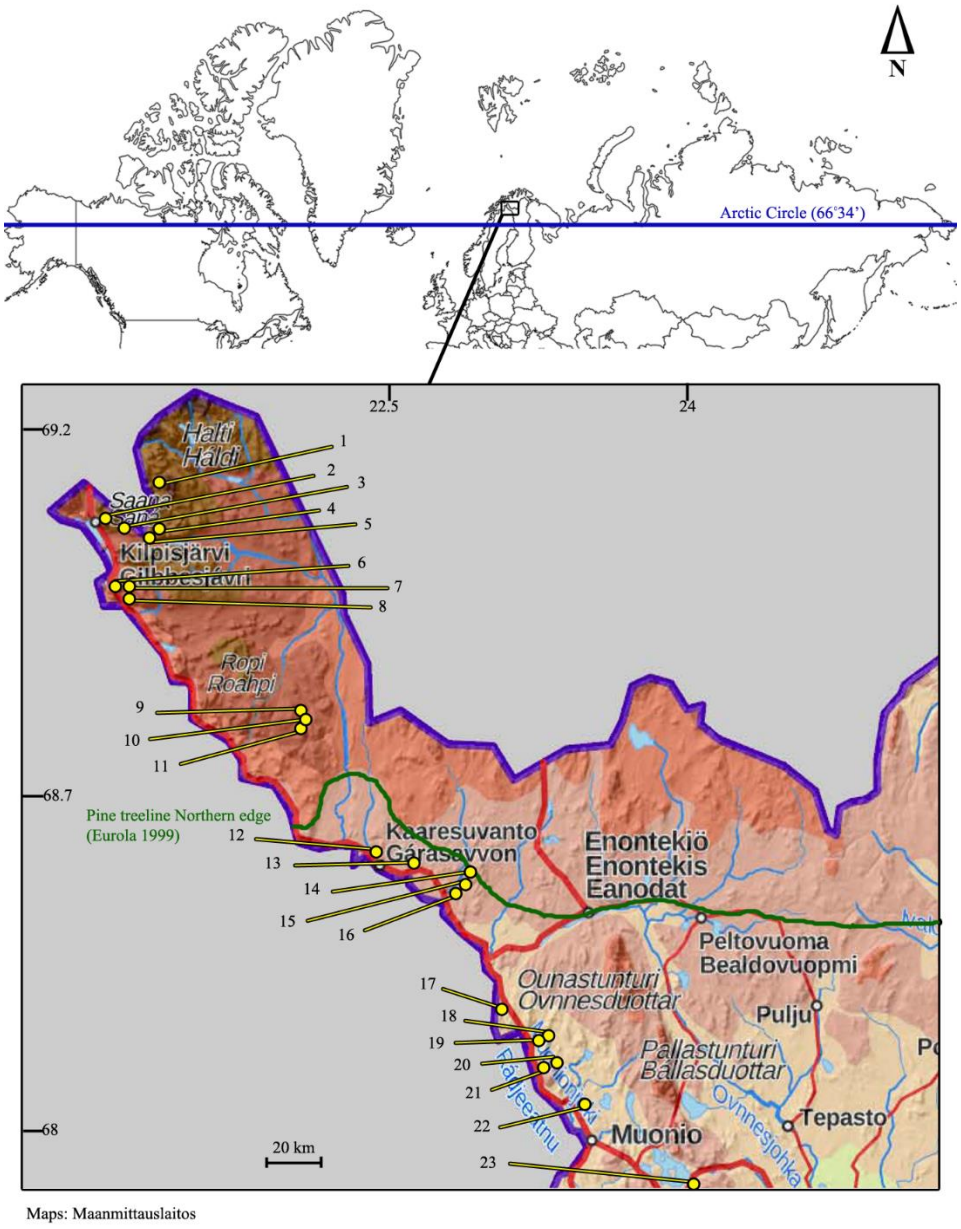


Figure 1. Locations of sampling sites 1-23.

Study area and description of sampling sites

The study sites (Figure 1.) are located on an annual average air temperature gradient with 2 °C increase from North to South. As the water temperatures largely reflect that of areal air temperatures, a similar gradient is expected of surface water temperatures with elevation taken into account (Livingstone et al. 1999). The altitude gradient between the highest and the lowest site is 760 meters.

The bedrock in the study area ranges from Paleozoic arkose quartzite (1, 2, 3) to Paleoproterozoic gabbronite (10), granodiorite (12, 22), quartz diorite (14, 15, 16), quartzite (17, 20, 21) and to Neoarchean tonalite (4, 5), tonalitic migmatite (6, 7, 8), arkose gneiss (13) and sericite quartzite (9, 11, 23) (GTK, Maankamara-map database, 2021). The Ice-cover period lasts approximately 240 (lakes 1-11) to 220 (lakes 12-23) days (SYKE SY751, 2005).

The catchment areas of the study sites consist of barren rocky tundra landscape (the northern high altitude lakes 1-5), mountain birch forest vegetation (6-11) and pine, birch and spruce forests within the northern boreal vegetation zone (the southernmost sampling sites 12-23) (Picture 1).

Picture 1. Vegetation cover gradient in the study area from rocky and barren landscape (left) to mountain birch woodland (middle) and the edge of the boreal forest zone with mixed spruce, pine and birch forest (right).

There is a high variation of total organic carbon TOC in the lake set, with an almost tenfold difference between the highest and lowest concentrations (Table 3). Nutrient concentrations of total nitrogen (TN) and total phosphorus (TP) vary from below the limit of detection (ultraoligotrophic) to 14 µg l^{-1} TP (mesotrophic) with a single eutrophic lake (100 µg l^{-1} TP) (Table 3). These features make this set of lakes ideal for studying effects of rising temperature and increasing carbon flux in subarctic lakes. More environmental information of the study sites is presented in Appendix 1.

Table 3. Limnological background information of sampling sites (Weckström, 1998, Unpublished data) and average air temperatures from two weather stations between years 1981-2010 (Finnish Meteorological Institute, 2021).

Lake (nr)	Co-ordinates	Altitude (m.a.s.l)	Area (ha)	Vegetation zone*	Max. depth (m)	Surface temp. July (°C)	pH	Cond. (µS cm^{-1})	TOC (mg l^{-1})	TN (µg l^{-1})	TP (µg l^{-1})
1	69°17'N 21°05'E	1009	9.6	Ba	12	7.8	5.6	5.9	1.1	110	L2
2	69°05'N 20°87'E	679	69.9	Ba	29	9.8	6.8	27.7	1.8	97	3
3	69°05'N 20°98'E	687	16.9	Ba	10.5	12.6	6.6	18.2	2.7	130	6
4	69°06'N 21°05'E	774	20.4	Ba	2.8	13.4	7	11.6	2.2	160	6
5	69°03'N 21°13'E	796	9.3	Ba	10.1	12.5	7	12.8	2.2	160	4
	69°02'N 20°47'E Kilpisjärvi, Finland 1981-2010 Annual average air temperature -1,9 °C (July 11,2 °C)										
6	68°92'N 20°97'E	526	3.9	MBW	2.1	12.9	7.2	37.7	8.9	-	-
7	68°92'N 21°05'E	596	3.5	MBW	10.1	14.7	6.8	13.3	3.2	180	5
8	68°90'N 21°07'E	463	6.1	MBW	2.1	15.5	6.9	23.9	7.3	260	6
9	68°68'N 22°05'E	526	13.9	MBW	6.4	10.9	7.4	28.0	4.9	-	-
10	68°67'N 22°05'E	498	10.3	MBW	17	11.1	7.5	33.5	6.5	-	-
11	68°67'N 22°03'E	508	1.4	MBW	2.85	9.8	7.3	32.8	4.8	-	-
12	68°47'N 22°43'E	322	2.6	SPB	4.2	17.0	6.3	11.9	6.0	320	8
13	68°42'N 22°58'E	332	2.0	SPB	1.85	16.8	4.4	13.5	9.5	430	10
14	68°42'N 22°90'E	319	28.2	SPB	7.1	16.7	7	29.3	7.3	340	14
15	68°40'N 22°88'E	317	2.6	SPB	6.40	13.4	6.5	6.4	4.2	-	-
16	68°40'N 22°85'E	313	2.2	SPB	4.1	17.5	6.6	9.4	7.1	400	8
17	68°20'N 23°18'E	263	0.9	SPB	5.00	14.3	6.5	16.0	7.2	-	-
18	68°13'N 23°37'E	253	1.3	SPB	4.3	17.9	4	5.2	8.5	460	11
19	68°12'N 23°37'E	252	1.5	SPB	4.4	17.7	6.2	6.4	8.2	1200	25
20	68°10'N 23°42'E	249	4.0	SPB	10.4	16.2	6	17.2	8.9	240	10
21	68°01'N 23°40'E	249	4.3	SPB	3.4	17.0	5.9	18.7	9.1	350	100
22	67°98'N 23°68'E	262	10.7	SPB	4	16.8	4.8	7.2	8.3	280	9
23	67°85'N 24°18'E	268	7.1	SPB	4	16.8	6.1	10.7	8.6	360	10
	67°25'N 26°35'E Sodankylä, Finland 1981-2010 Annual average air temperature -0,4 °C (July 14.5 °C)										

*Ba = barren above the tree line; MBW = mountain birch woodland; SPB = spruce, pine and birch forest

Sampling

Sampling was conducted during the first week of September 2020 in northwest Finnish Lapland. Sediment samples were derived from the deepest basin of the lake using a HTH Kajak corer (Renberg & Hansson, 2008). The top-bottom approach (e.g. Michelutti et al. 2001; Weckström et al. 2003) was used to maximize the spatio-temporal resolution. The sediment layers 0-1 cm and 10-11 cm were collected from each lake and placed in small plastic bags. These layers are thought to represent modern time and pre-industrial conditions, respectively based on the known slow sedimentation rate in the area (e.g. Sorvari, 2001; Korhola

& Weckström 2004). The sample bags were stored in dark and cool as soon as possible after sampling to avoid degradation of organic sediment material, especially pigments. Eventually, the pigment samples were stored frozen before sending them for pigment analysis to the Environmental Change Laboratory, University of Nottingham, UK.

Pigment analysis

Pigments were extracted quantitatively from sediment in 80:15:5 solvent mixture of acetone: methanol: water. Extracts were kept overnight in -10 °C then filtered with PTFE 0.2 μm filter and dried with N_2 gas dryer. A predetermined quantity was re-dissolved into 70:25:5 injection solution of acetone: ion-pairing reagent of 75 mg/l tetra butyl ammonium acetate and 770 mg/l of ammonium acetate water solution: methanol, and injected into the HPLC unit (High Precision Liquid Chromatography). Agilent 1200 series module with quaternary pump was used for separations. The solid stationary phase consisted of 205 x 4.6 mm, 5 μm particle size Thermo Scientific ODS Hypersil column. Mobile phase included 80:20 methanol: 0.5 M ammonium acetate Eluent A, 9:1 acetonitrile: water Eluent B and ethyl acetate Eluent C. Elution began with 100 % Eluent A with gradual transition to 100 % Eluent B over 4 minutes. For the next 34 minutes the proportion of Eluent C was gradually increased to 75 %, 25 % B and 75 % C was held for 1 minute and it was followed by 4 minute back-transition to 100 % Eluent A (Chen et al. 2001). Analytes passed through a photo-diode array detector, where UV-visible spectral properties were analyzed between 350 and 750 nm. Pigment quantification was based on calibration with DHI Denmark standards and peak areas scanned at 435 nm. Original results of pigment per unit of dry weight of sediment were normalized by dividing them with the percentage of organic matter (OM%). Concentrations are reported as molecular weight of pigment per unit OM weight of sediment.

Loss on ignition (LOI)

Loss on ignition analysis was conducted according to Heiri et al. 2001 in order to determine the organic matter content of the collected 46 samples. Samples were weighed wet in pre-burned (15 minutes in 550 °C) crucibles, then dried overnight in a warm cabinet (105 °C) and weighed for dry mass. Dry samples were then burned in a muffle oven at 550 °C for 4 hours, left to cool in an exicator for 30 minutes, and weighed for mineral mass. Organic matter percentage was calculated as loss on ignition divided by dry weight.

Statistical analyses

One-way ANOVA analyses

The surface and bottom pigment samples were compared in order to determine the general trends of change using one-way ANOVA with post-hoc two tail t-tests assuming equal variation, and corrected with Bonferroni- correction to decrease uncertainty. Analyses were performed with Microsoft Excel.

Pearson correlation test

Cyanobacterial pigment data correlation with environmental variables was analyzed using the Pearson correlation test with Students' two-tail t-test. Analyses were performed with Microsoft Excel.

Ordination analysis of pigment-environment data

Prior to statistical analysis environmental variables (excluding pH) were log10(x + 1) transformed and pigment data were square-root transformed. Out of the original 20 measured environmental variables, 12 were chosen for the final statistical analyses after screening with Variance Inflation Factor (VIF). Environmental variables with VIF-values <20 were included in addition to environmental variables with ecological importance. As the gradient length of the first detrended correspondence analysis (DCA) axis was 1.9 SD units indicating a linear response of the pigment data to the environment, a linear approach, namely principal components analysis (PCA), was used to determine the main patterns of variation within the 23 lake pigment data. In order to reveal the relationships between pigment and environmental data (Jan Weckström, unpublished data 1998), redundancy analysis (RDA) was conducted (as the first axis gradient length in DCA was 0.9 SD). In RDA, the 23 surface samples were added as active response variables, whereas the 21 bottom samples were added as supplementary (passive) samples. Moreover, the vegetation zones were added as nominal (passive 0/1) variables. Statistical significance was tested using Monte Carlo permutation test (999 permutations). Both PCA and RDA were performed using CANOCO for Windows version 5.01 (ter Braak & Šmilauer, 1997–2012). Pigments from the top- and bottom samples were expressed as nanomole/g dry weight/percentage of organic matter in altitudinal order using the software C2 1.7.7 (Juggins, 2007) (Fig. 11).

Uncertainties

In this study, the exact timeline of change cannot be studied due to the top-bottom sediment sampling method. Thus this study focuses on analyzing broader trends and change from pre-industrial to modern times by analyzing change in pigment concentrations of the topmost 0-1 cm and 10-11 cm sediment layers.

Sedimentary degradation is always an issue when studying sediment material. Pigment preservation decreases due to exposure to light, temperature, oxygen and microbial degradation (Florian et al. 2015). The sampling procedure could thus have increased pigment degradation through exposure to light and oxygen. *In situ* light exposure could have also had an effect on pigment preservation at very shallow or clear-water sites with high water transparency Moreover, due to the slow sedimentation rates in the area (Sorvari, 2001) planktic pigments might have degraded even during the settling process (Florian et al. 2015). Few sites are impacted by groundwater inflow, which could also affect sediment preservation and settling processes. Of the studied pigments most labile are chl *a*, chl *b* and echinenone (McGowan et al. 2005; Deshpande et al. 2014; Krajewska et al, 2018). Both OM% normalization and chl *a*: pheophytin *a*– ratio validation were, however, used to screen results for potentially problematic/unreliable samples (see results, page 19, Figure 2 & Figure 3).

Lutein (chlorophytes) and zeaxanthin (cyanobacteria) could not be distinguished from each other in HPLC chromatogram. Thus a decision was made to use the data and discuss the concentrations as cyanobacterial zeaxanthin to have even a rough estimate of amount of picocyanobacteria (Deshpande et al. 2014). In addition, several potentially toxin-producing cyanobacteria genera could not be studied, as they do not produce group-specific pigments. Picocyanobacteria is a group mostly formed of harmless species (Lizotte, 2008), occurrence of harmful genera, for example *Microcystis*, could not be separately studied. Similarly, identified non-heterocystous filamentous toxin-producer genera (eg. *Oscillatoria, Phormidium, Planktothrix* and *Leptolyngbya*) could not be studied.

Results

Sediment organic matter content and Chl *a* : Pheophytin *a*-ratio

Organic matter percentages of sediment samples are presented in Figure 2. OM % appears to increase from north to south with a range from 12 % to 91 % in the bottom sediment samples and from 18 % to 85 % in the surface sediment samples. The southernmost sampling sites show no clear indication of higher OM content in the surface sediment compared to the lower (bottom) sample. In lakes number 1, 3, 4, 5, 9 and 11, the surface sediment has notably higher OM % with an average increase of 17 %.

The Chlorophyll *a* : Pheophytin *a* ratio is used to assess pigment degradation and hence to validate pigment data (Deshpande et al. 2014). If the ratio is < 1, it indicates poor pigment preservation (Deshpande et al. 2014). The Chl *a* : Pheophytin *a*-ratio was < 1 in four bottom sediment samples (1, 2, 11, 19)(Figure 3). Thus, results from these samples should be interpreted with caution.

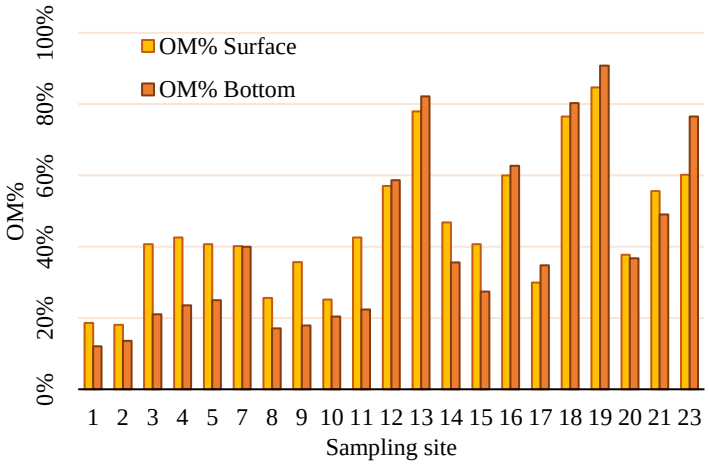


Figure 2. Organic matter percentages of 42 sediment samples.

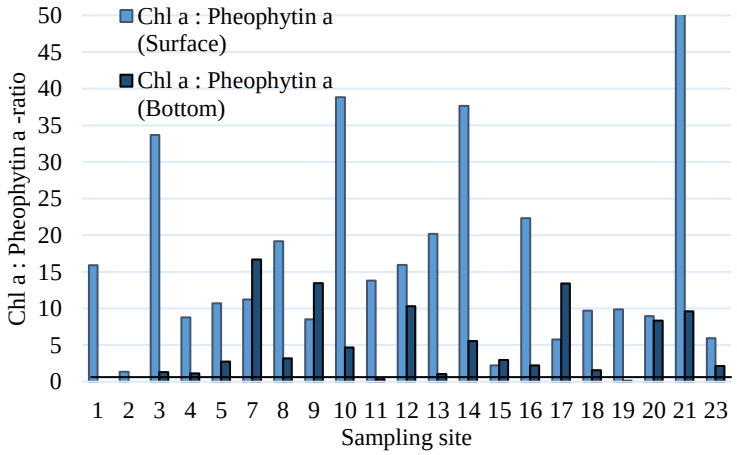


Figure 3. Chlorophyll *a* : Pheophytin *a* ratios of 42 sediment samples. Black line marking y-axis value 1.

Primary production and producer group specific pigments

Chlorophyll *a* is common indicator of primary production (McGowan et al. 2005; Deshpande et al. 2014). Chl *a* concentrations showed site specific variation ranging from 14.5 to 3850 nmol g OM^{-1} in surface samples (average 602 nmol g OM^{-1}) and from 0 to 715 nmol g OM^{-1} in bottom samples (average 115 nmol g OM^{-1}) but indicated a general trend of increased primary production (Figure 4). Surface and bottom sample concentrations were significantly different in two tail t-test with Bonferroni correction ($p < 0.01$).

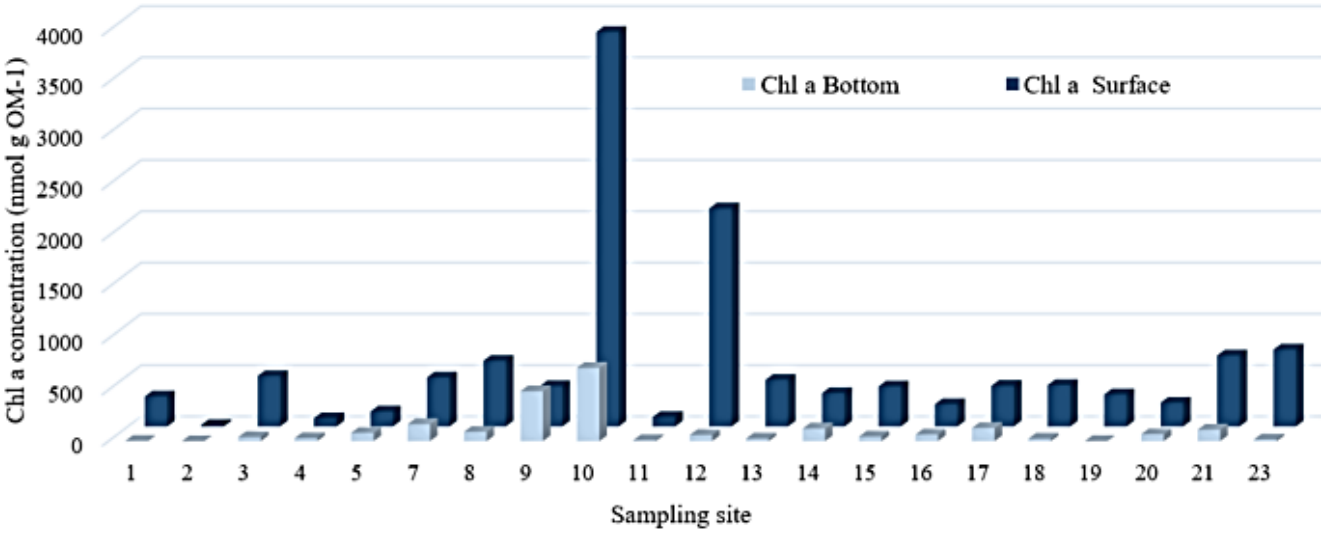


Figure 4. Chlorophyll *a* concentrations of surface and bottom sediment samples.

Pheophytin *a* concentrations (Figure 5) ranged from 6.77 to 178 nmol g OM^{-1} in surface samples (average 41.2 nmol g OM^{-1}) and from 0 to 154 nmol g OM^{-1} in bottom samples (average 25.8 nmol g OM^{-1}) and showed no significant difference between surface and bottom samples ($p > 0.05$).

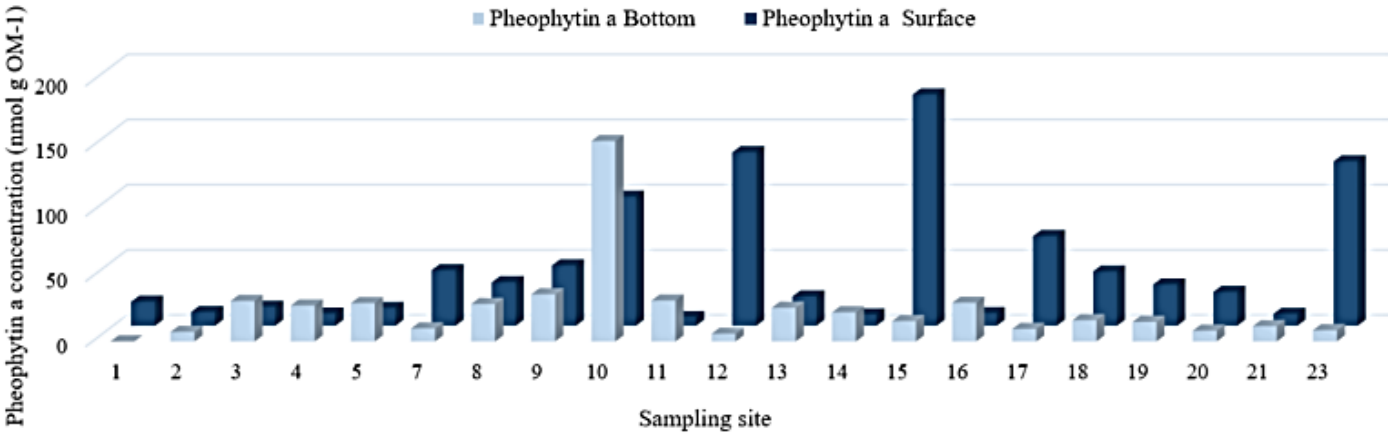


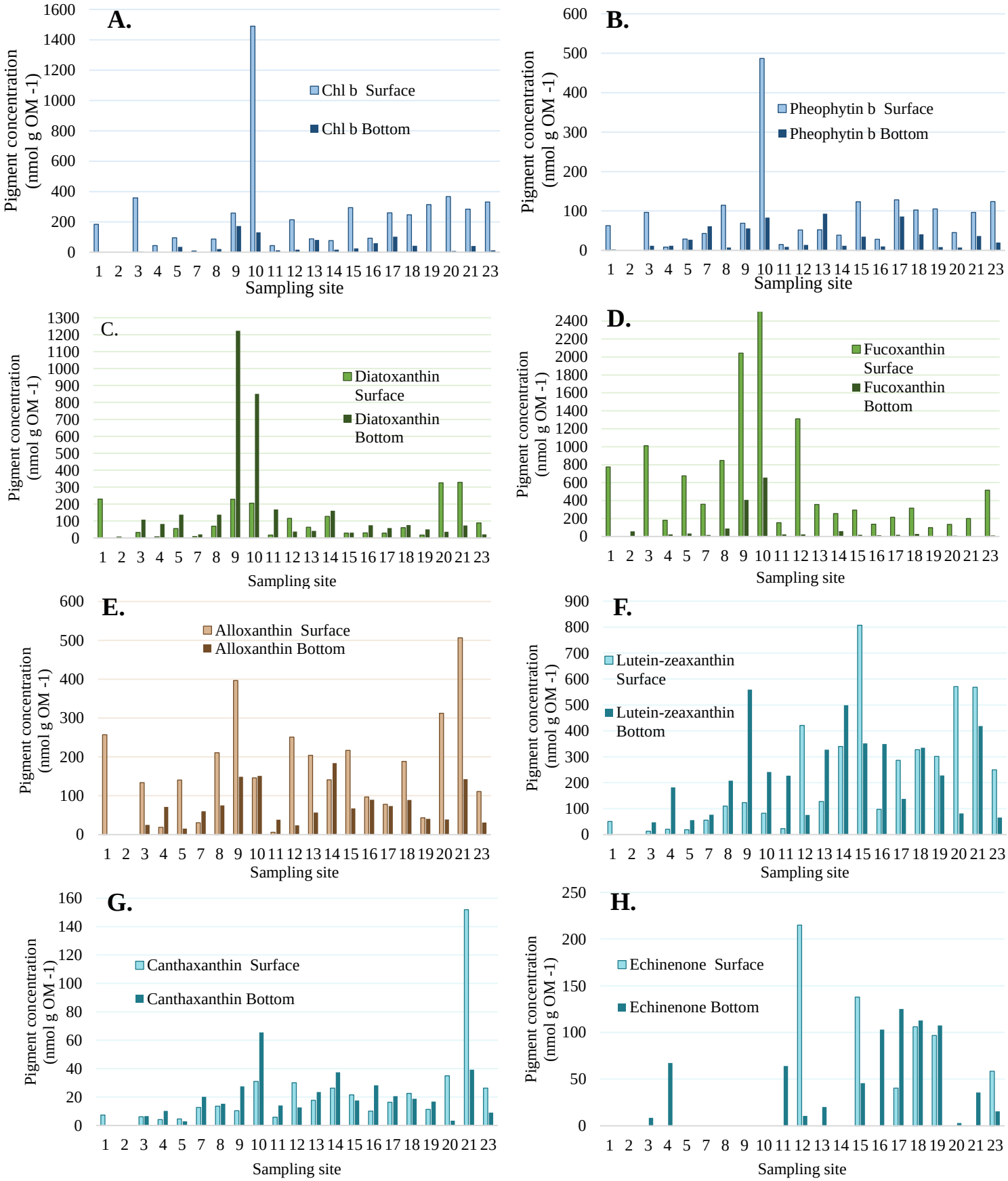
Figure 5. Pheophytin *a* concentrations of 44 surface and bottom sediment samples.

Group-specific pigment concentrations are presented in figures 6 A-H. Chlorophyte-specific pigments chlorophyll *b* (Figure 6A) and pheophytin *b* (Figure 6B) have increased in surface samples with average increases of 49.7 nmol g OM^{-1} and 56.7 nmol g OM^{-1} respectively. Both had a statistically significant difference between surface and bottom samples with p-values < 0.01 for chlorophyll *b* and p < 0.025 for pheophytin *b*. Chlorophyll *b* ranged from 0 to 1490 nmol g OM^{-1} in surface samples (average 240 nmol g OM^{-1}) and from 0 to 173 nmol g OM^{-1} in bottom samples (average 38.2 nmol g OM^{-1}). Pheophytin *b* ranged from 0 to 487 nmol g OM^{-1} in surface samples (average 84.8 nmol g OM^{-1}) and from 0 to 93.3 nmol g OM^{-1} in bottom samples (average 30.5 nmol g OM^{-1}).

Diatom-specific pigments fucoxanthin (Figure 6C) and diatoxanthin (Figure 6D) have differing trends. Fucoxanthin ranged from 0 to 8120 nmol g OM^{-1} in surface samples (average 874 nmol g OM^{-1}) and from 0 to 656 nmol g OM^{-1} in bottom samples (average 74.0 nmol g OM^{-1}). Fucoxanthin has increased from bottom to surface samples with an average increase of 786 nmol g OM^{-1} and the difference was statistically significant (p < 0.01). Diatoxanthin, however, appeared to have increased in some sites and decreased in others varying from 5.0 to 328 nmol g OM^{-1} in surface samples (average 99.2 nmol g OM^{-1}) and from 0 to 1220 nmol g OM^{-1} in bottom samples (average 168 nmol g OM^{-1}). No significant difference was found.

Cryptophyte-specific alloxanthin (Figure 6E) shows an increasing trend with an average increase of 98.5 nmol g OM^{-1}, which is statistically significant (p < 0.01). Alloxanthin concentrations ranged from 0 to 506 nmol g OM^{-1} in surface samples (average 169 nmol g OM^{-1}) and from 0 to 184 nmol g OM^{-1} in bottom samples (average 69.5 nmol g OM^{-1}).

Cyanobacterial pigments lutein-zeaxanthin (Figure 6F) (see also page 18, Uncertainties), canthaxanthin (Figure 6G), and echinone (Figure 6H) show site-specific variation between surface and bottom samples. Lutein-zeaxanthin ranged from 0 to 807 nmol g OM^{-1} in surface samples (average 217 nmol g OM^{-1}) and from 0 to 559 nmol g OM^{-1} in bottom samples (average 220 nmol g OM^{-1}). Canthaxanthin ranged from 0 to 152 nmol g OM^{-1} in surface samples (average 21.9 nmol g OM^{-1}) and from 0 to 65.6 nmol g OM^{-1} in bottom samples (average 19.1 nmol g OM^{-1}). Echinenone ranged from 0 to 215 nmol g OM^{-1} in surface samples (average 29.8 nmol g OM^{-1}) and from 0 to 125 nmol g OM^{-1} in bottom samples (average 35.2 nmol g OM^{-1}). No significant general increasing trend could be observed.



Figures 6 A-H. Top-bottom comparison of analyzed chlorophyte (A & B), siliceous algae (C & D), cryptophyte (E) and cyanobacteria (F-H) pigments.

Relative pigment distributions

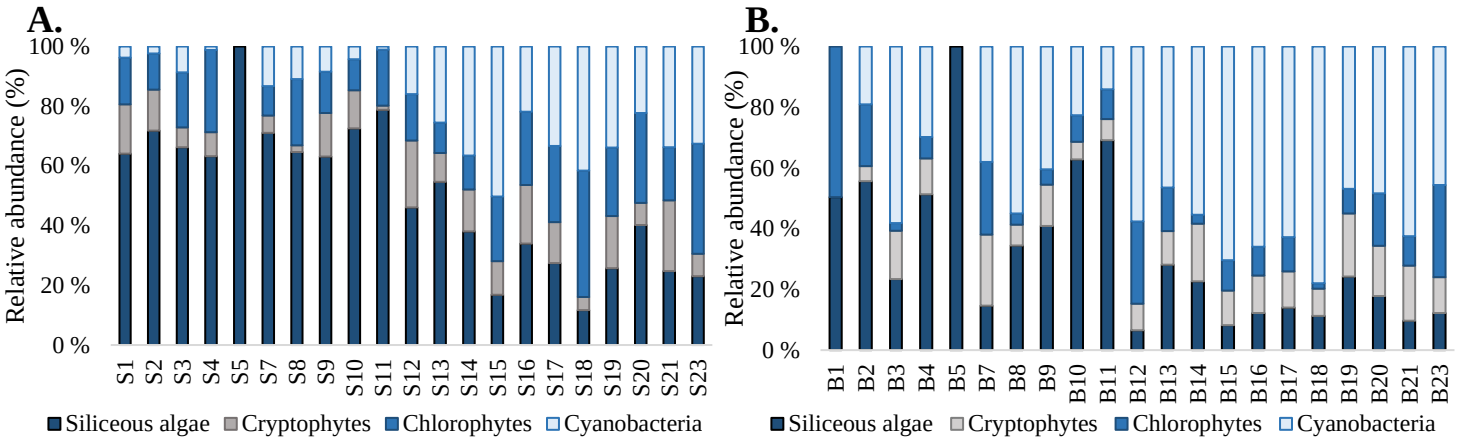
Relative pigment distributions (Figures 7 A, B) indicate an increase of relative diatom abundance in most of the sites (average increase in relative abundance of diatom-related pigments 19 %). The relative abundance of chlorophytes has also increased with an average increase in their pigments of 6.7 %. The relative abundance of cryptophytes has stayed the same. The relative abundance of cyanobacteria has decreased (average decrease in the relative abundance of their pigments 26 %).

Average relative pigment distributions and changes in distributions differed between vegetation zones. In the Ba zone (sites 1-5) surface samples, relative abundance of siliceous algal pigments varied from 63 to 72 % (average 66 %), cryptophyte pigments from 6.6 to 16 % (average 11 %), chlorophyte pigments from 12 to 28 % (average 18 %) and cyanobacterial pigments from 1.1 to 8.6 % (average 4.0 %). In the bottom samples, relative abundance of siliceous algal pigments varied from 23 to 56 % (average 45 %), cryptophyte pigments from 0 to 16 % (average 8.2 %), chlorophyte pigments from 2.6 to 50 % (average 20 %) and cyanobacterial pigments from 0 to 58 % (average 28 %). Relative abundances of siliceous algal and cryptophyte pigments have increased from bottom samples to surface samples on average by 21 % and 3 %, respectively. Relative abundances of chlorophyte and cyanobacterial pigments have decreased on average by 1.4 % and 23 %, respectively.

In the MBW zone (sites 7-11) surface samples, relative abundance of siliceous algal pigments varied from 63 to 79 % (average 70 %), cryptophyte pigments from 1.4 to 15 % (average 7.3 %), chlorophyte pigments from 10 to 22 % (average 15 %) and cyanobacterial pigments from 1.1 to 13 % (average 7.6 %). In the bottom samples, the relative abundance of siliceous algal pigments varied from 12 to 69 % (average 44 %), cryptophyte pigments from 5.7 to 23 % (average 11 %), chlorophyte pigments from 3.7 to 24 % (average 10 %) and cyanobacterial pigments from 14 to 55 % (average 34 %). The relative abundances of siliceous algal and chlorophyte pigments have increased from the bottom samples to surface samples on average by 26 % and 4.8 %, respectively. Relative abundances of cryptophyte and cyanobacterial pigments have decreased on average by 4 % and 26 %, respectively.

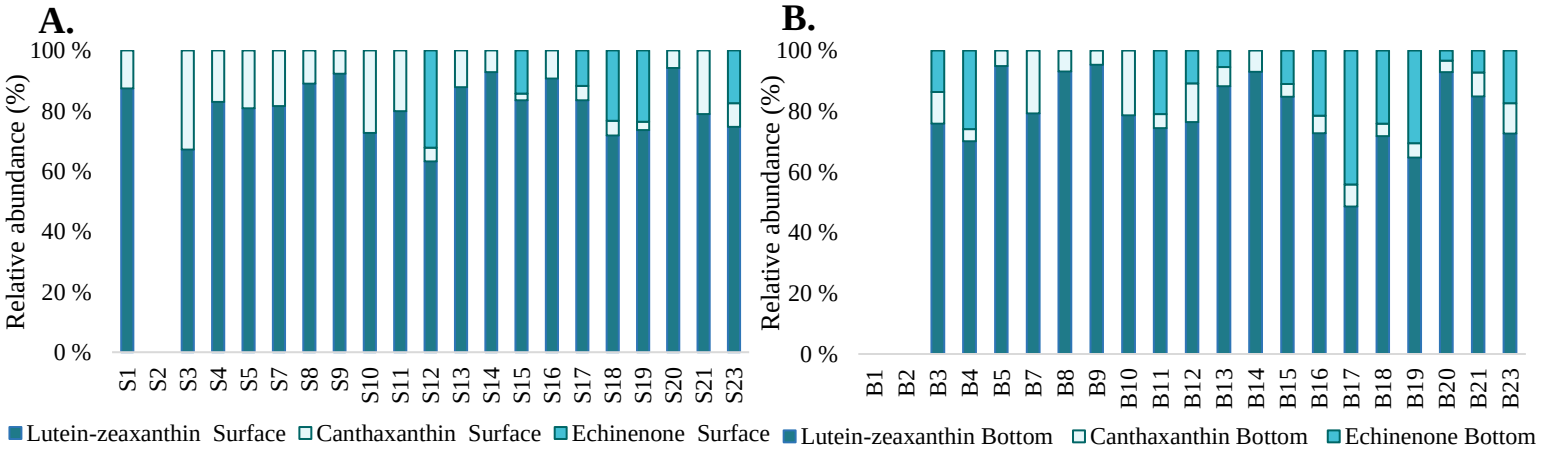
In the SPB zone (sites 12-23) surface samples, relative abundance of siliceous algal pigments varied from 12 to 55 % (average 31 %), cryptophyte pigments from 4.4 to 24 % (average 14 %), chlorophyte pigments from 10 to 42 % (average 24 %) and cyanobacterial pigments from 16 to 50 % (average 32 %). In the bottom samples, the relative abundance of siliceous algal pigments varied from 6.5 to 28 % (average 15 %), cryptophyte pigments from 8.8 to 21 % (average 14 %), chlorophyte pigments from 1.8 to 30 % (average 13 %) and cyanobacterial pigments from 46 to 78 % (average 58 %). The relative abundances of siliceous algal and chlorophyte pigments have increased from the bottom sample to surface sample on

average by 16 % and 11 %, respectively. The average relative abundances of cryptophytes stayed the same. The relative abundances of cyanobacterial pigments have decreased on average by 27 %.



Figures 7 A&B. Relative pigment distribution by producer groups in 23 surface (A) and 21 bottom (B) sediment samples.

Cyanobacterial pigment distributions have changed slightly from bottom to surface samples (Figures 8 A, B). The average relative abundance of canthaxanthin appears to have increased towards north with 16 %, 5.5 % and 0.8 % increases in Ba, MBW and SPB zones, respectively. The relative abundance of echinone decreased towards north with a 9.9 % decrease in Ba, 4.2 % decrease in MBW, and 4.8 % decrease in the SPB zone. The relative abundance of zeaxanthin appears to have increased most in the Ba zone (19 %), but decreased by 1.1 % in the MBW zone, and slightly increased in the SPB zone (4%). As echinenone is more labile than zeaxanthin and canthaxanthin (Krajewska et al. 2018), the abundances of the latter two were compared with each other. Average ratios of zeaxanthin to canthaxanthin were: 4.2 in surface and 14 in bottom samples of in the Ba zone; 5.6 in surface and 12 in bottom samples of the MBW zone; and 16 in surface and 13 in bottom samples of the SPB zone.



Figures 8 A&B. Relative cyanobacterial pigment distribution in surface (A) and bottom (B) sediment samples of 21 sites.

Ordination analyses

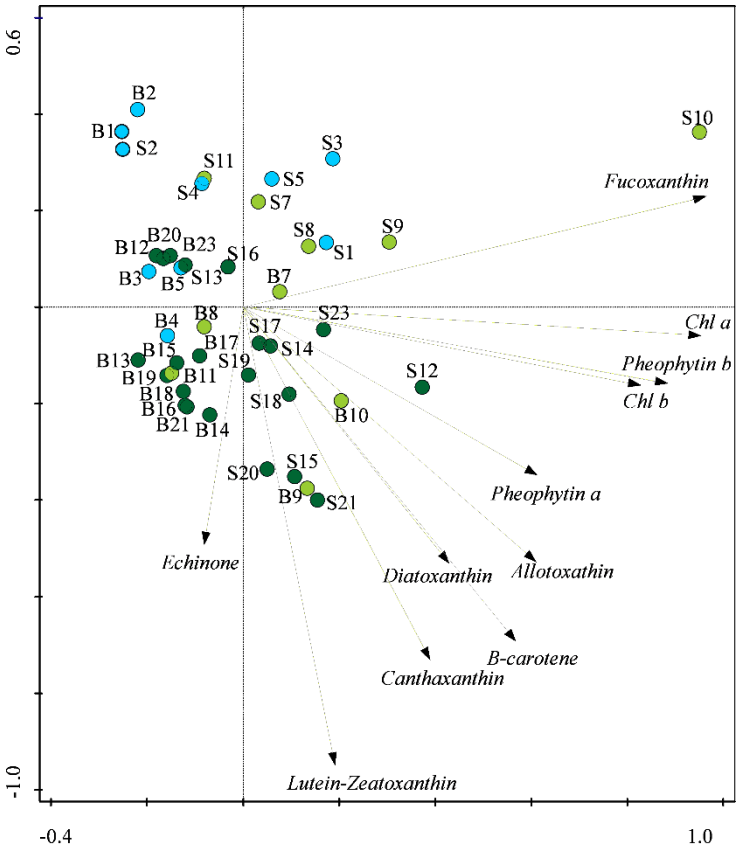


Figure 9. PCA biplot of 21 sampling sites and pigment data. Sampling sites are split to three groups based on location in vegetation zone: blue describing barren, light green describing mountain birch woodland and dark green describing spruce, pine and birch forest zone.

In PCA, the sampling sites are mainly clustered by vegetation zones and the productivity gradient from barren to forested catchments. However, some overlapping and shifts between the bottom and surface samples can also be observed (Figure 9).

Ba zone sites are mostly clustered in the top left corner of the PCA biplot, the MBW zone sites are spread in the middle to middle-right and the SPB zone sites are mostly clustered in the lower side of the bi-plot. Pigment concentrations are increasing towards the opposite direction of the Ba zone cluster, which is logical considering the minimal effect of barren catchments on productivity. Most notable changes appear to have occurred within the MBW zone and the SPB zone sites. Of the MBW zone sites 9 and 10, the surface sediment sample positions have moved towards the top right corner from the bottom samples. Of the SPB zone sites 12, 20 and 21, the surface samples have moved towards the bottom right corner and towards higher pigment production.

RDA (as PCA) displays a clear zonation of samples based on vegetation zones (Figure 10). Based on the position of the surface samples and the passively plotted bottom samples, many sites have undergone changes along the productivity gradient indicated by TOC and LOI (OM %). RDA axis 1 explained 70 %, and RDA axis 2 explained 15.6 % of variation within the response data.

RDA axis 1 was most influenced by alkalinity, conductivity, and potassium (K) concentration. RDA axis 2 was most influenced by air temperature, mire area, the amount of organic matter, and lake area (Figure 10).

The results of RDA support previous observations of increased production as many surface samples (1, 2, 5-7, 12, 14-16, 18-23) have shifted along the productivity gradient from the top left to the bottom right quadrant (Figure 10). Some sites (e.g. 9, 10) indicate a community shift towards a diatom-controlled system.

Sites 8 and 13 could indicate a recovery from acidification. Some sites (12, 15, 20, 21 & 23) have shifted towards higher cyanobacteria abundance. This can also be seen in figures 6 F-H. Curiously, site 18 has also shifted towards environmental conditions preferred by cyanobacteria, but based on pigment data cyanobacterial abundances have not increased.

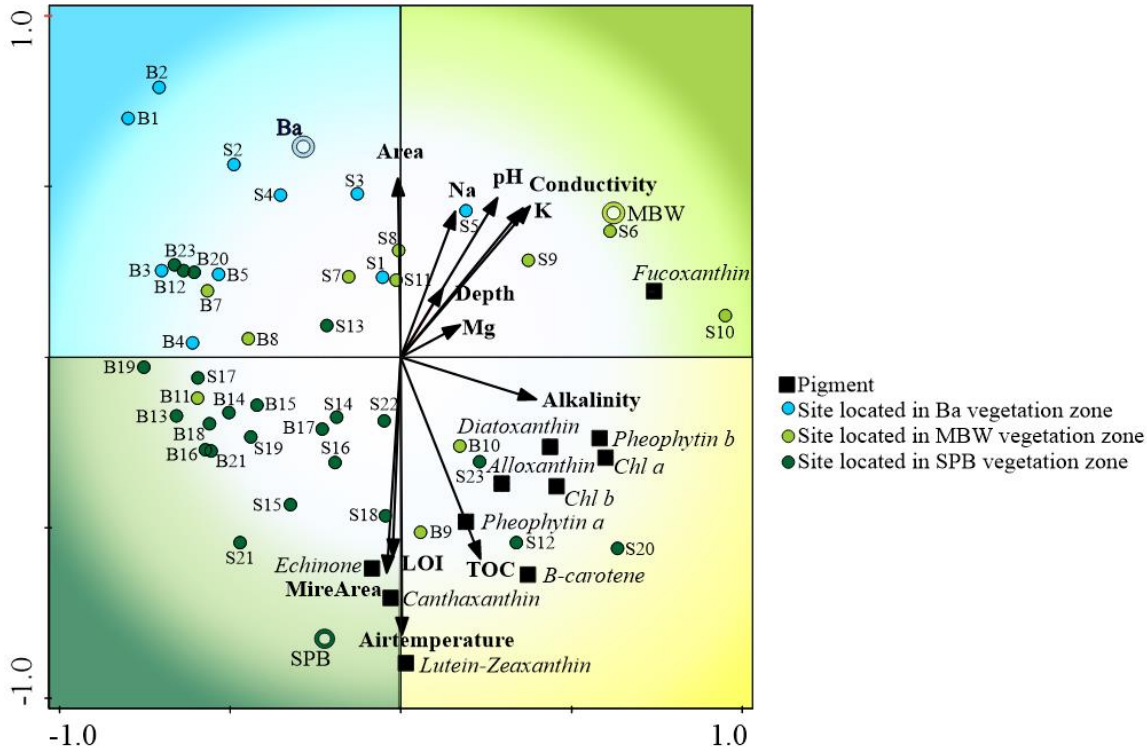


Figure 10. RDA of 23 sampling sites, pigment data and vegetation zones. Vector map is split to four areas based on vegetation zone and amount of productivity: blue describing barren, light green describing mountain birch woodland, dark green describing spruce, pine & birch forest zone and yellow describing zone of high productivity.

Figure 11, presenting the pigment concentrations of the top and bottom samples, supports the results of the RDA and clearly shows an increase in productivity towards the SPB vegetation zone. The most notable producer group in the Ba zone appear to be siliceous algae with intermediate cryptophyte and low chlorophyte and cyanobacterial pigment concentrations, in the surface samples. The MBW zone is characterized by high siliceous algal and chlorophyte productivity (sites 9 and 10) with relatively low cryptophyte and cyanobacteria pigment concentrations. The SPB zone has the most evenly distributed producer group pigment concentrations with cyanobacteria, siliceous algae and chlorophyte pigments occurring at high concentrations. Highest concentrations of cryptophyte-produced alloxanthin occurs also in the SPB zone.

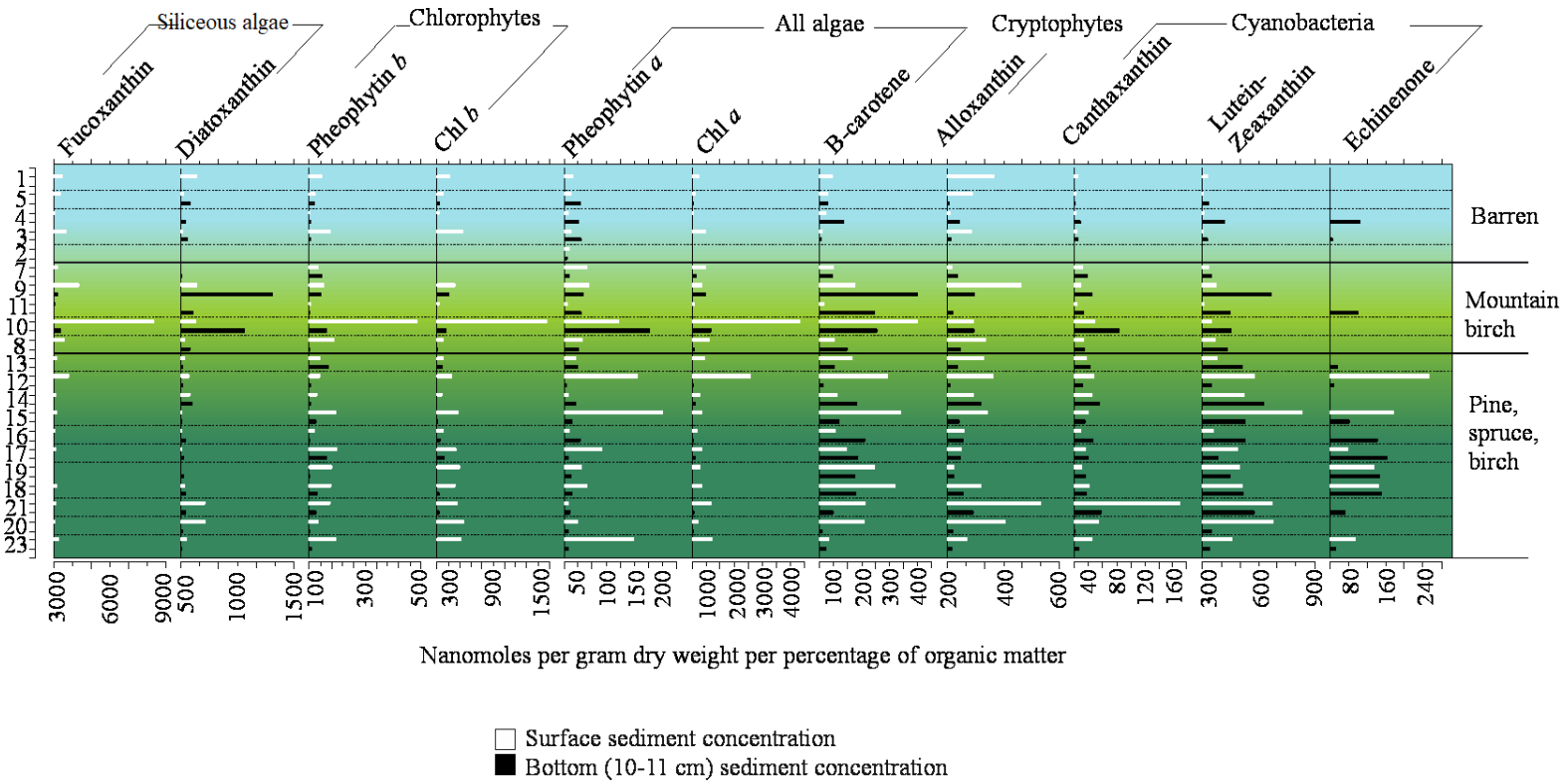


Figure 11. Top-bottom samples of pigment concentrations ordered by vegetation zones and productivity. Blue describing Ba, light green describing MBW and dark green describing SPB zone.

As indicated by the RDA, cyanobacterial pigments are significantly correlated with a variety of environmental variables. The Pearson correlation test revealed a significant positive correlation between echinone concentrations and bottom water temperatures, OM %, and a significant negative correlation with sodium (Na) concentrations (Table 4). Canthaxanthin concentrations were significantly positively correlated with alkalinity, mire area and TP. Lutein/Zeaxanthin concentrations were significantly positively correlated with surface water temperature, TOC, TP, and negatively correlated with altitude.

Table 4. Most important environmental variables affecting cyanobacterial pigment concentrations and correlation coefficients by Pearson correlation test with Students' two-tail t-test. Bold coefficients mark statistically significant correlation ($p < 0.05$).

	Echinenone	Canthaxanthin	Lutein/Zeaxanthin
Alkalinity	-0.18	**0.57**	0.52
Altitude	-0.40	-0.41	**-0.73**
Surface water temperature	0.41	0.34	**0.62**
Bottom water temperature	**0.54**	-0.03	0.04
OM%	**0.51**	0.12	0.39
Mire area	0.13	**0.54**	0.47
Na	**-0.54**	0.21	-0.08
TOC	0.26	0.44	**0.71**
TP	-0.04	**0.96**	**0.59**

Discussion

Algal communities

The general trends in algal communities over the past ca. 150 years varied depending on the vegetation zone. An overall trend of increased primary production however, was observed throughout the vegetation gradient. Similar observations have also been made by other studies (e.g. Lami et al. 2010; Florian et al. 2015). The barren vegetation zone sites 1, 2 and 4 showed no particularly notable change, whereas sites 3 and 5 show a clear increase in productivity seen as an increase in the abundance of siliceous algae, cryptophytes and chlorophytes. The MBW zone, site 11 did not show any notable change in pigment concentrations and sites 7, 8, 9 and 10 showed increased concentrations of pigments related to chlorophytes, cryptophytes, and especially siliceous algae. However, it must be noted that fucoxanthin indicating high abundances of siliceous algae is chemically rather unstable (susceptible to light, oxidation, acid and basic conditions (Komba et al. 2018)) and has been found in surface sediments in misleadingly high concentrations, when compared to deeper sediment layers (Krajewska et al. 2018). Based on the RDA, the changes in the Ba and MBW zones appear to be linked to increasing alkalinity/decreasing pH and increasing conductivity (linked to an increase in ions K, Na, and Mg). The abundance of cyanobacteria is generally decreasing in these sites. The increase of chlorophytes indicates higher temperatures (Florian et al. 2015), and could also indicate riparian shrubification i.e. greening (Wrona et al. 2016).

The increased primary production of these two vegetation zones is most probably climate driven and related to temperature-regulated ice- and snow-cover dynamics (Smol et al. 2005; Vincent et al. 2008A; Wrona et al. 2016). Decreased ice-cover thickness and increased length of the growing have been found to increase phytoplankton production (Smol et al. 2005) and to cause a shift from benthic production towards a more productive water column (Vadeboncoeur et al. 2003). White ice (ice mixed with snow), however, can decrease under-ice plankton production (Vincent et al. 2008A; Wrona et al. 2016). The impact of such light inhibition might be compensated by the lengthened growing season due to shortened ice-cover duration (Wrona et al. 2016). Ice regimes also affect lake thermal structure (Vincent et al. 2011). Clear-water Arctic lakes are often isothermal, i.e. they are not stratified during summer (Sorvari et al. 2002). Shorter ice cover periods, however, can result in stronger stratification in deep lakes and in greater mixing in shallow lakes (Vincent et al. 2008B; Wrona et al. 2016). These changes would benefit planktic species such as buoyant filamentous cyanobacteria preferring to inhabit the layer between top and bottom water and on the other hand, smaller planktic species dependent on mixing and water movement to stay afloat (Paerl & Paul, 2012; Beaulieu et al. 2013). For benthic species stronger stratification could promote, for example, nutrient

deficiency or shading by planktic algae and greater mixing could increase sediment resuspension (Wrona et al. 2016), thus inhibiting light penetration via more turbid water column and sediment particles settling on top of the benthic communities. Increased concentrations of terrestrial material, such as humic substances, nutrients, and ions could result from increased precipitation and influx via increased runoff (Smol et al. 2005).

In the SPB zone, sites 13 and 14 show a similar trend of diatom, cryptophyte and chlorophyte increase possibly linked to to increased ion concentrations, pH, conductivity and alkalinity as suggested by RDA. Sites 16 and 19 show no notable increase in primary production or specific algal group. Sites 12, 20 and 23 all revealed markedly increased surface sediment pigment concentrations including all studied producer groups, and RDA suggests that this change is related to increased TOC. Similarly, sites 15, 18 and 21 show a notable increase of algal pigments, which seems to be correlated with increased TOC, temperature and mire area. Thus, lake browning appears to have influenced these sites. A general trend of increased primary production and lake browning could be observed in the SPB zone. This result contradicts Wrona et al. (2016), who suggested in their study that the magnitude of OM influx determines a lake either to become more productive or to undergo browning. This phenomenon could be explained by the "water color optimum", in which the influx of organic matter provides nutrients for primary producers and protects them from exposure to too high short-wave light and UV radiation without inhibiting light harvesting too much. In deeper lakes, browning can increase the length and strength of the stratification period and thus promote e.g. hypolimnium anoxia and internal loading (Snucins & John, 2000). Colored water can absorb more heat and the shallow warm euphotic zone can be notably warmer than the rest of the water column, providing optimal conditions for e.g. colonial planktic cyanobacteria (Snucins & John, 2000).

Feuctmayr et al. (2019) studied the combined impacts of brownification and climate warming on eutrophic temperate lakes. They found no net impact on gross primary production, respiration or net ecosystem production. Phytoplankton biomass, however, was found to decrease in DOC concentrations over 10 mg l^{-1}, but intermediate concentrations of ~7 mg l^{-1} promoted especially cyanobacterial blooms. The theory of browning increasing cyanobacterial abundance was supported by the results of this study. In this study – where the lakes range from ultraoligotrophic to mesotrophic – the nutrient and/or temperature impact via DOC influx is probably more significant and promotes higher rates of cyanobacterial production compared to the study by Karlsson et al. (2005), who found increased temperature and consequent increase of influx of terrestrial OM to increase primary production in Swedish high latitude subarctic lakes. They found a strong positive correlation between primary production and DOC concentration as well as between primary production and total nitrogen concentration (Karlsson et al. 2005). In this study, chlorophyll *a* or pheophytin *a* concentrations were not highly correlated with TOC or total nitrogen, having highest positive correlations

with temperature instead. Reuss et al. (2010) studied phototroph communities using sedimentary pigments in a survey of 100 Swedish subarctic lakes and found a strong negative correlation between DOC and benthic primary production. Their results strongly support the idea of DOC affecting primary production via reduced light and they concluded that in the studied lakes light availability was the major regulating factor of primary production (Reuss et al. 2010). Results of this study, however, indicate fast community recovery and partial replacement of primary producer groups if sites have undergone loss of benthic producers. Vesterinen et al. (2016) have found highly colored Finnish boreal zone lakes to be dominated by littoral benthic producers. This finding could explain why no decrease in primary production was observed in this study at sites where browning appears to be more marked.

In addition, the increase in DOC has been found to enhance bacterial plankton domination of lake metabolism, to modify autotrophic primary production by changing the chemical and physical environment, as well as to decrease nutrient availability due to complexation of nutrients like phosphorus or iron (Jones, 1992). The chemical nature of DOC influx must also have an effect in how it impacts lakes – microbial OM degradation might also increase in aquatic ecosystems due to warming temperatures and could increase availability of OM-bound nutrients transported from the catchment. As lake browning is predicted to continue in the study region in the future (Seppä & Weckström, 1999; de Wit et al. 2016; Finer et al. 2020), more information on chemical signatures and the role in nutrient input of DOC in the subarctic region should be gathered to provide better estimates of impacts of browning on lakes in the future.

Cyanobacterial abundances

Cyanobacteria communities appeared to have undergone marked changes. In the more northern Ba and MBW vegetation zone lakes (1-11), cyanobacteria appear to have almost disappeared from algal communities. Historical pigment concentrations in these sites indicate that cyanobacteria have been an important part of these algal communities with relative cyanobacterial pigment abundances on average 27 % in the Ba zone and 34 % in the MBW zone. They have markedly declined during the last c.a. 150 years to average relative abundances of 4 % in the Ba and 7.6 % in the MBW zone. Assuming these past communities have mostly consisted of benthic mat-forming cyanobacteria – as is typical for Arctic lakes (Bonilla et al. 2005; Vincent & Quesada, 2012) – reasons for their abundance decline could be e.g. changes in the light environment, loss of competition advantage, or an unfavorable N/P-ratio. According to Bonilla et al. (2005), benthic mat communities are often regulated by light availability. Climate warming- enhanced changes in ice and snow cover causing changes in the light environment could thus be the main reason behind the disappearance of benthic cyanobacteria as they might favor planktic production (Vadeboncoeur

et al. 2003; Wrona et al. 2016). Another explanation could be an unfavorable nitrogen to phosphorus ratio (N/P-ratio). As mat communities often contain nitrogen-fixing species, they are better able to compete for phosphorus in the water column, while other algae might be limited by the lack of nitrogen (Lizotte, 2008; Vincent & Quesada, 2012). Climate warming and an increased precipitation-enhanced influx of organic carbon (OC) could thus cause loss of this competition advantage by added influx of organic nitrogen, as OC and organic nitrogen cycles are strongly connected (Finer et al. 2020). This, however, is not supported by zeaxanthin to canthaxanthin-ratios, which indicate an increase in the relative proportion of filamentous nitrogen-binding species both in the Ba zone (modern ratio 4.2 and historical ratio 14.4) and in the MBW zone (modern ratio 5.6 and historical ratio 11.5). In addition, there might be other yet unknown changes in these lakes causing loss of competition advantages or inhibiting cyanobacterial growth. Jungblut et al. (2010) found Arctic and Antarctic cyanobacteria to present extreme cold ecotypes, which have evolved during up to 10 million years to withstand these harsh environmental conditions. It could be possible that these evolved growth and life strategies are not competitive in the current changing environment.

The increase in cyanobacteria was mainly observed in the SPB zone sites 12, 15, 20, 21 and 23. However, cyanobacteria dominance of algal communities in all SPB zone sites combined has decreased with relative cyanobacterial pigment abundances declining from a historical average of 58 % to the modern average relative abundance of 32 %.

Sites 12, 15, 20, 21 and 23 are characterized by increased TOC, temperature and mire area values and are suspected to have undergone significant browning. Carvalho et al. (2011) surveyed a 134 lake dataset from the United Kingdom and found a cyanobacterial peak in lakes with water-color values around 10 – 20 Pt l^{-1}. Similarly, Feuctmayr et al. (2019) found intermediate DOC concentrations of ~7 mg l^{-1} promoting cyanobacterial blooms. The concentrations of TOC in the SPB sites (n = 12) were on average 7.7 mg l^{-1} and half of the sites had notably higher abundances of cyanobacteria. Groundwater-impacted lakes (17 and 19), acidic lakes with a pH < 4.5 (13 and 18), and clear lakes located in sandy esker areas (14, 16 – lake 15 explained later) did not have high abundances of cyanobacteria, which supports the hypothesis that cyanobacteria increase in sites undergoing browning. Browning can provide multiple competition advantages for cyanobacteria. In shallow littoral zones and the warm surface water layer, colored water absorbs more heat and thus provides a warmer habitat for cyanobacteria. Simultaneously, colored water often stratifies more strongly. Cyanobacteria tend to thrive in warmer temperatures (Pal et al. 2015), are capable of buoyancy control (Beaulieu et al. 2013), and are able to utilize DOC as a nutrient source (Tittel et al. 2009).

Human-enhanced cyanobacteria increase

In addition to climate change-induced browning, human activity likely influenced cyanobacterial abundance in some lakes. Lake 12 (Figure 12, a) is a small mire lake located close to a road and housing, which could lead to nutrient import from either the surrounding mire or human activity close by. Lake 15 (Figure 12, b) is located in a sandy esker area but has a small beach. When comparing lake 15 to similar lakes 14 and 16 close by, it appears that even slight human activity can have a distinct impact on the algal community of these type of lakes. This impact is most likely caused by a slight nutrient enrichment by the beach users. The catchment areas of lakes 20 and 21 (Figure 12, c, d) have been influenced by intensive forestry activity during recent decades. Based on RDA, lake 20 has experienced a dramatic shift from a lake comparable to lakes in the Ba zone to a highly productive system. On a catchment scale, lake 20 has received the highest load of OC influx of all the study lakes. A change this dramatic implies significant anthropogenic influence and indicates that intensive forestry has a severe impact on lakes located close by.

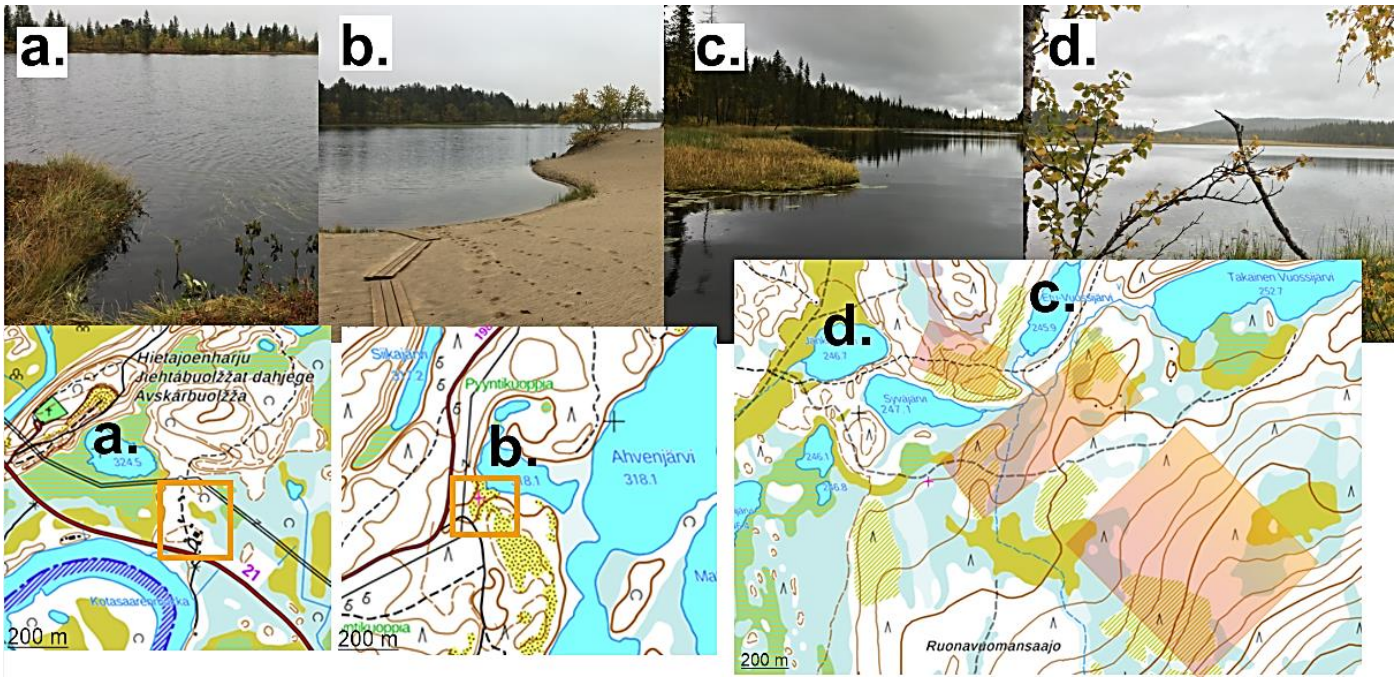


Figure 12. Pictures and locations of lakes 12 (a), 15 (b), 20 (c) and 21 (d). In maps housing (12), beach (15) and intensive forestry (20 & 21) are marked with orange. Maps Retkikartta.fi (4.5.2021).

The surface sediment sample position of lake 21 in the RDA had moved further toward the cyanobacteria-pigment abundant zone and had highest concentrations of canthaxanthin out of all studied lakes as well as high concentrations of other pigments. Lake 23 appeared to be the only site with no significant human impact but it still has undergone a notable increase in cyanobacteria abundance. Lake 23 is located close to a mire, thus changes in mire hydrology and OM degradation could explain the increased influx of OC and

increase of cyanobacteria. Site 22 had very similar concentrations of algal pigments as site 23, including cyanobacteria, and was located in a catchment of mires and mixed spruce, pine and birch forest with forestry activity. The bottom sample of site 22 was not analyzed, but the results from these lakes with similar environmental settings indicate a similar trend.

Factors controlling cyanobacteria abundance

Rigosi et al. (2014) and Elliott (2012) point out that the strength of temperature and nutrient enrichment impact is reliant on the trophic status of the lake, which functions as a base for a potential increase in cyanobacteria. Oligotrophic lakes were found to be more sensitive to nutrient influence, whereas mesotrophic lakes were more sensitive to temperature change (Rigosi et al. 2014). In addition, cyanobacteria increase is dependent on species present in the ecosystem affected. Rigosi et al. (2014) determined genus-specific sensitivities to either nutrient or temperature increase with *Lyngbya, Merismopedia*, *Microcystis* and *Oscillatoria* being more sensitive to temperature increase, and *Anabaena, Aphanizomenon, Coelosphaerium, Croococcus, Phormidium* and *Synechococcus* being more sensitive to nutrient enhancement. However, as cyanobacteria often vary in size, growth and photosynthetic rates, nitrogen fixing capability or gas vesicles even within a specific genus (Whitton & Potts, 2012), it is possible for species to react differently to environmental changes even within a specific genus.

In this study three cyanobacterial carotenoids were studied: 1) echinenone produced by all cyanobacteria (McGowan et al. 2005; Krajewska et al. 2018), 2) canthaxanthin produced by heterocystous filamentous cyanobacteria (Krajewska et al. 2018), and 3) zeaxanthin produced by picocyanobacteria (Deshpande et al. 2014; Krajewska et al. 2018). Echinenone was correlated positively with bottom water temperature, OM % and negatively with Na concentrations. Canthaxanthin had a high positive correlation with TP and positive correlations with alkalinity and mire area. Zeaxanthin (Read Uncertainties, page 18) had positive correlations with surface water temperature, TOC, TP, and a negative correlation with altitude.

Functional groups and cyanobacteria genera

Studied carotenoids fluctuated site specifically emphasizing the need to better understand genera-specific reactions and individual responses of studied lakes to changing environmental variables. However, few general trends and responses could be observed.

Lake 21 has the highest phosphorus concentration (100 µg l^{-1} TP) and the highest concentration of canthaxanthin (152 nmol g OM $^{-1}$) with a relatively low TN/TP-ratio. This indicates high abundance of *Anabaena* and/or *Nostoc* species. These genera can either be filamentous mat, film or aggregate formers, or planktic, freely floating communities. Algal primary producers require nitrogen and phosphorus in certain ratios. The demand of nitrogen is higher relative to phosphorus, but phosphorus is often, especially in freshwater ecosystems, the limiting nutrient (Lyons & Finlay, 2008). Heterocystous cyanobacteria usually benefit from nitrogen depletion in the water column. This is often the case especially in the early growing season, which also increases the likelihood of nitrogen limitation later in the year, and thus further promotes the dominance of cyanobacteria (Figure 13) (Elliott, 2012). However, as OC and nitrogen cycles are highly correlated in the study area, lakes containing higher amount of TOC often have higher amount of organic nitrogen as well. Thus, nitrogen limitation of the water column is more likely dependent on higher phosphorus input, which is supported by the results of this study, especially when comparing site 21 to sites 20 and 23.

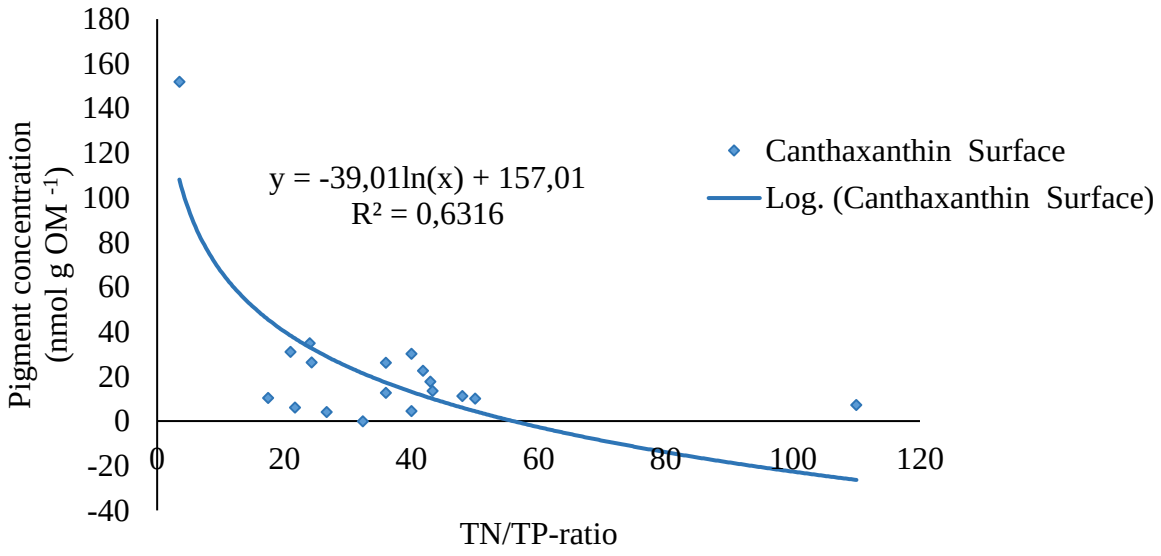


Figure 13. Canthaxanthin and TN/TP-ratio relationship describes how nitrogen fixing cyanobacteria increase when TN/TP-ratio decreases.

Zeaxanthin concentrations were highest in lakes 15, 20 and 21, with lakes 12, 14, 17-19 and 23 having moderate concentrations. Zeaxanthin concentrations were positively correlated with surface water temperature, TOC, TP and negatively correlated with altitude. These correlations and genus preferences by Rigosi et al. (2014) indicate that *Synechococcus*, the generally most common genus of picocyanobacteria in Arctic lakes (Lizotte, 2008), might not be the dominating genus in the picocyanobacteria communities of these lakes. This is supported by the high correlation of temperature and altitude, which suggests that other genera such as *Microcystis* could dominate small-sized cyanobacteria abundances.

Echinenone concentrations were highest in lakes 12, 15, 18 and 19. The lack of echinenone in sites indicating high to intermediate cyanobacteria abundance via canthaxanthin or zeaxanthin concentrations (e.g. sites 13-14 and 20-21) was rather unexpected, but indicates that echinenone is either too labile to be used as an indicator of all cyanobacterial production or indicates the presence of other cyanobacterial genera not included in the functional groups studied. Positive correlations with OM and bottom water temperature as well as negative correlation with Na could indicate the presence of genera such as *Oscillatoria, Cylindrospermopsis* or *Planktothrix*, as genera *Anabaena, Microcystis, Nostoc* and *Lyngbya* are generally more tolerant to salinity (Paerl & Paul, 2012; Vincent & Quesada, 2012).

Based on the decrease of cyanobacteria in the Ba zone, the appearance of low concentrations of the mostly picocyanobacteria-specific pigment zexanthin in the MBW zone, and the increased abundance of cyanobacterial pigments in the southernmost sites, it appears that cyanobacteria communities are shifting from cold-ecotype benthic mats (Jungblut et al. 2010) to low abundances of planktic picocyanobacteria and heterocystous filamentous species (Vadeboncoeur et al. 2003), and further on to highly abundant planktic and littoral benthic communities (Keva et al. 2020). This cyanobacteria community shift is especially worrying due to the aggressive growth and blooming capacity of planktic cyanobacteria. It is, however, also a notable threat considering possible habitat losses for benthic grazers and possible changes in the food-web structures of subarctic lakes.

Toxic cyanobacterial blooms

Cyanobacteria are present in lake ecosystems throughout the year, but when opportunities arise massive planktic blooms can break out. These usually occur during late summer or autumn (Lee 2008). Massive planktic blooms are often associated with cultural eutrophication and other anthropogenic activities changing physical and biogeochemical characteristics in waterbodies (Whitton & Potts 2012, Oliver et al. 2012). As previously mentioned, browning can induce cyanobacterial blooms (Carvalho et al. 2011; Feuctmayr et al. 2019). Factors promoting toxin production in cyanobacteria still largely remains a mystery. Sivonen & Jones (1999) concluded that optimal conditions for cyanobacterial blooms are also optimal conditions for toxin production for planktic cyanobacteria.

As shown by Vesterinen et al. (2016), cyanobacteria can dominate even colored lakes via high littoral abundances. Toxin production and bloom formation of this type of mat communities are still poorly understood. Heath & Wood (2010) found no evidence of environmental variables or mat coverage

correlating with toxin concentrations. They concluded that, as toxic and non-toxic genotypes of the same species are present in the mats, the relative amount of each genotype seems to vary rapidly for unknown reasons and thus concentrations of toxins fluctuate (Heath & Wood, 2010). During blooms, the toxin concentrations are higher either due to a higher amount of cyanobacterial cells or due to more favorable environmental conditions that promote toxin production (Quiblier et al. 2013). Kaebernick and Neilan (2001) studied microcystin synthesis of polar mat forming cyanobacteria and determined that temperature had a significant effect on toxin production. They showed that the optimal temperature for microcystin synthesis is 20 °C. Kleinteich et al. (2012) studied polar cyanobacteria growth in a variety of temperatures and concluded that the optimal growth rate for toxin producing species is achieved at temperatures between 8-16 °C. As studied lakes in the SPB zone have July surface water temperatures close to the microcystin synthesis optimum, it is possible that sites with high cyanobacteria abundances have experienced toxic blooms. Browning-induced warming of littoral and surface water could possibly increase the toxicity of cyanobacterial blooms in the subarctic in the future.

Environmental concentrations of cyanotoxins

In Europe, planktic cyanobacterial blooms have been monitored closely due to their potential threat to water security. In Italy, the monitoring period of 2004 revealed that extra-cellular concentrations of MCs ranged between 0.004 – 226 μg l^{-1} and CYN between 0.3 – 126 μg l^{-1} (Messineo et al. 2009). Monitoring of cyanotoxins in the environment has focused mainly on observing planktic blooms. Heath et al. (2011) observed cyanotoxin concentrations produced by benthic cyanobacteria in New Zealand rivers for a year and found highest concentrations (21.7 μg l^{-1}) of ATX-a during the stable water phase at the end of the summer at a temperature of 14 °C. Mez et al. (1998) observed cyanotoxin concentrations in alpine lakes for a three-month summer period and found the highest concentrations of MC-LR to be 2 μg l^{-1}. Kleinteich et al. (2013) studied STX and MC presence in Arctic lakes and found the operon gene stxA in one out of five samples. This sample of the mat contained 21 μg STX kg^{-1} dw. All samples contained the MC-producing gene mcyA with variants of MC (including MC-RR in one sample with a concentration of 106 μg MC kg^{-1} dw). Producers of STX were suspected to be *Lyngbya* or *Scytonema* species, but the MC-producing gene was so abundant that no specific genus could be identified to be the probable producer (Kleinteich et al. 2013). In a later environmental DNA (eDNA) study targeting 16S rRNA, Kleinteich et al. (2018) found *Nostoc* sp. to be the most likely producer of MCs in all of the studied 26 mat samples. Trout-Haney et al. (2016) studied MC concentrations of 18 lakes in Greenland during summers 2013-2015 and measured concentrations ranging from 0.005 to > 0.4 μg l^{-1}, with a median of 0.057 μg l^{-1}.

As both benthic and planktic cyanobacteria communities have been found to contain cyanotoxins even in the high Arctic, it is highly likely that the cyanobacteria communities of the lakes studied here include toxin-producing strains of cyanobacteria and contain toxins during bloom events. The heterocystous filamentous cyanobacteria group includes two genera that are well known for toxin-producing species found in Finland: *Nostoc (*e.g. benthic *N. spongiaformis)* and *Anabaena* (e.g. *A. flos-aquae, A. lemmemannii, A. lapponica*) (Sivonen & Jones, 1999). Zeaxanthin-producing picocyanobacteria in the study area most likely include *Microcystis* species, especially at the warmer end of the temperature gradient (Lizotte, 2008). Known MC-producing species of the genus *Microcystis* found in Finland include, for example, *M. aerunginosa, M. viridis* and *M. flos-aquae* (Sivonen & Jones, 1999). The cyanobacteria pigment concentrations in surface sediments of sites 20 and 23 indicate likely blooms of *Microcystis* sp., or blooms formed by other small-sized cyanobacteria. Sites 15 and 21 on the other hand could produce either, or mixed blooms of *Anabaena* sp., *Nostoc* sp. and/or e.g. *Microcystis* sp. In addition, high echinone concentrations in sites 12 and 15 do not appear to indicate either picocyanobacteria or heterocystous filamentous cyanobacteria, and could (instead) indicate high abundances of other cyanobacteria genera (e.g. toxin-producing *Cylindrospermopsis, Oscillatoria, Phormidium, Planktothrix* or *Leptolyngbya*).

In addition to a wide dispersal of toxin producers and possible growth enhancement by the changing environment, browning can inhibit photodegradation of cyanotoxins by preventing penetration of short-wave radiation. As photodegradation is believed to be the main degradation pathway for microcystins, browning could promote higher concentrations of microcystins during the bloom events (Quiblier et al. 2013). This could be significant especially in the studied brown-water lakes. However, the quality of OC influx causing browning may play an important role. Klitzke et al. (2011) suggest that cyanotoxins have a high tendency to adsorb to OM or clay particles. Thus, the quality of OC influx can greatly determine the possible effect browning has on cyanotoxin degradation. In the study area, on average 90 % of TOC consists of DOC indicating low potential for adsorption to OM particles (available data n=11, Jan Weckström, unpublished data 1998). Some bacteria species capable of biodegradation of cyanotoxins have been found from temperate and tropical lakes (Corbel et al. 2013), and biodegradation of cyanotoxins might be a significant removal pathway especially in highly productive systems.

Implications to aquatic ecosystems

Various studies have discussed other toxicological effects of especially the most harmful variant microcystin-LR (MC-LR). Qiao et al. (2016) studied MC-LRs effects on the reproduction of the female medaka fish (*Oryzias latipes*) by exposing the fish to 1 μg l^{-1} and 5 μg l^{-1} pure MC-LR and to *Microcystis*

aeruginosa extract that had an equivalent of 5 μg l^{-1} concentration of MC-LR for 28 days. All concentrations had adverse effects on the medaka fish females' reproduction with the extract from *M. aeruginosa* having a wider range of harmful impacts on reproductive biological pathways. The authors suggested that even concentrations of 1 μg l^{-1} could be harmful to aquatic organisms. Hou et al. (2015) studied the effect of MC-LRs on reproduction and endocrine disruption on zebrafish (*Danio rerio*) females by a life cycle exposure of 90 days with concentrations of 0.3, 3, and 30 μg l^{-1} of MC-LR. They observed growth inhibition, decreased ovary weight, ovarian ultra-pathological lesions and decreased ovarian hormone levels. Some damage-compensating methods were observed but the impaired development and reproduction of female zebrafish was significant (Hou et al. 2015). Wu et al. (2016) studied developmental neurotoxicity of MC-LR on zebrafish embryos by exposing the embryos to 0.8, 1.6, and 3.2 μg l^{-1} concentrations of MC-LR and found delayed hatching, decrease in body length, significant decrease in dopamine and acetylcholine content and accumulation of MC-LR to the larvae. Unlike in laboratory studies, the natural environment tends to contain a "cocktail" of toxins. Drobac et al. (2016) studied fishponds in Serbia that had experienced severe cyanobacterial blooms and found saxitoxin, nodularin and microcystins in the ponds. In all of the blooming ponds the studied species common carp (*Cyprinus carpio*) had histopathological damage to liver, kidney, gills, intestines and muscle tissues (Drobac et al. 2016).

However, several studies suggest that aquatic organisms have a high tolerance to cyanotoxins (Ibelings & Havens, 2008; Chislock et al. 2013; Combes et al. 2013). Combes et al. (2013) studied ciliates (*Nassula* sp.) feeding exclusively on a MC-producing strain of *Planktothrix agardhii* over a period of eight months. Ciliates were able to feed and grow during the study period, even though they showed slower growth rates and higher concentrations of antioxidants than the control cultures (Combes et al. 2013). Similarly, Chislock et al. (2013) studied a natural strain of water fleas (*Daphnia pulicaria*) and their ability to control toxin-producing cyanobacteria abundances. In two eutrophic lakes dominated by *Microcystis* sp. and *Anabaena* sp., water fleas were able to reduce phytoplankton biomass by 76 % and 80 %, even when MC concentrations exceeded 100 μg l^{-1} (Chislock et al. 2013). These studies indicate that natural genotypes of aquatic organisms are more capable of tolerating microcystins than previously thought based on laboratory studies.

Effects of cyanobacterial blooms are not limited to the threat to water security, but blooms can also impact lake community composition by a switch to algal communities dominated by cyanobacteria. This can markedly change the structure and trophic functions of a lake and the energy flow of the entire ecosystem (Oliver et al. 2012; Šulčius et al. 2017; Keva et al. 2020). Šulčius et al. (2017) studied the effect of harmful cyanobacteria blooms to ecosystems by using collected extracts.. They found differing toxicological effects of extracts without a clear relationship to known toxin concentrations or biomass and different reactions

between different organisms exposed to the same extract. Šulčius et al. (2017) found evidence of toxic cyanobacteria blooms having direct and indirect effects causing changes in food-web structure and ecosystem function. Keva et al. (2020) studied possible future changes in the food webs of Finnish subarctic lakes due to environmental forcing by climate change and concluded that the warming climate and increasing productivity will promote community shifts to systems dominated by cyanobacteria and cyprinid fish – shifts, which appear to be persistent against restoration. They further found forestry and other anthropogenic activity to enhance these community shifts. Keva et al. (2020) estimate larger-scale community shifts to take place further in the future, as these are thought to be dependent on a vegetation shift to pine forests in the catchment areas of lakes (Keva et al. 2020), which would require ca. 2.5 °C higher July average air temperatures (Kultti et al. 2006).

In this study, the relative abundance of cyanobacteria in algal communities has decreased on average in all vegetation zones. Increased cyanobacterial pigment concentrations were concentrated to the SPB zone and connected to lake browning as well as human activity. The highest cyanobacteria proportion was found in the SPB zone site 15, which had a relative cyanobacterial pigment abundance of a 50 % (SPB average 32 %). The increased cyanobacterial pigment concentrations were similar to concentration levels found in the Baltic Sea sediments from known bloom areas (Krajewska et al. 2018), thus indicating the potential for formation of toxic cyanobacteria blooms. The possible blooms of e.g. *Anabaena* sp., *Nostoc* sp. and/or *Microcystis* sp. could have high potential to produce cyanotoxins during bloom events. In addition, the brown waters might protect toxins from photodegradation and enhance toxicological effects. The toxic blooms might already have changed the food-web structures by favoring toxin- and turbidity-tolerant species and ecosystem function by enhancing internal nutrient loading as well as promoting hypolimnium anoxia in the sites showing increased cyanobacteria abundance.

Future prospects

Based on the development of the cyanobacteria abundance in different vegetation zones during the last approximately 150 years, a succession theory presented by Keva et al. (2020) appears to be accurate. Browning in addition to climate change-induced warming and changes in mixing and thermal dynamics as well as in ice and snow cover appear to drive lake ecosystems towards higher cyanobacteria abundances and increased primary production. Increased primary production could increase productivity of the entire ecosystem and further shift the ecosystems towards a scenario of cyanobacteria- and cyprinid fish-dominated communities as described by Keva et al. (2020). However, cold-ecotype benthic cyanobacteria appear to have declined in the most northern sites in the Ba and the MBW zones and the less abundant

modern cyanobacteria communities in these lakes appear to be mostly dominated by picocyanobacteria. It is possible that this shift from abundant benthic communities to less abundant picocyanobacteria communities is the first step in a succession towards systems strongly controlled by cyanobacteria. The time scale of such a succession is difficult to estimate, noting especially the time required for the pine tree line and forests to grow and spread further north. In high Arctic benthic cyanobacteria-dominated lakes, the shift to siliceous algae-dominated algal communities and picocyanobacteria-dominated cyanobacteria communities however might occur relatively soon as the Arctic is rapidly warming.

Recent harmful toxic cyanobacterial bloom observations have been made in both oligotrophic and mesotrophic lakes, late fall blooms observed in diatom-controlled lakes, episodic blooms observed in rivers and invading tropic cyanobacteria species have been observed in Canada (Pick 2016; Favot et al. 2019). Favot et al. (2019) found warmer air temperatures, declined wind speed and lengthening of the ice-free season to promote *Dolichospermum* sp. blooms and a coinciding decline in oxygen concentrations in a Canadian oligotrophic lake. Similarly Smucker et al. (2021) connected cyanobacterial blooms to earlier and longer warming of surface water, earlier onset of stratification and longer durations of hypolimnium hypoxia. Yan et al. (2017) suggest that a positive feedback loop exists between cyanobacterial blooms, eutrophication and global warming. In a microcosm system study, Yan et al. (2017) found large concentrations of chemically available phosphorus and nitrogen released to the water column during decomposition of cyanobacteria, thus further promoting the eutrophic state of the lakes. Decomposition lowers dissolved oxygen levels, pH, reductive conditions and produces a large amount of CH_4 and CO_2, with methane being responsible of up to 92 % of the emitted mass of carbon (Yan et al. 2017).

Based on predictions and observations of increases in lake productivity, cyanobacteria abundance in algal communities, harmful cyanobacterial blooms and related ecosystem food-web and function impacts, it is of utmost importance to prevent these shifts of ecosystem state. As these changes are connected to global warming, cultural eutrophication and anthropogenic land use, mitigation of greenhouse gas emissions, nutrient pollution and development of new innovative methods to control erosion is crucial. If no action to protect these unique freshwater ecosystems is taken, consequences for water security, food security, biodiversity and cold-water ecotypes are predicted to be severe.

Conclusions and further study

Subarctic algal communities in the study area have changed during the last ca. 150 years. A general trend of increased primary production was observed throughout all three vegetation zones. Few of the Ba zone cyanobacterial communities show no change, whereas the rest of the sites show an increase in siliceous

algae, cryptophytes and chlorophytes, and a decline in cyanobacteria abundance. The MBW zone communities have generally developed from cyanobacteria- and siliceous algae-dominated communities to communities dominated by siliceous algae, cryptophytes and chlorophytes. The SPB zone sites all showed increased primary production and half of the sites showed increased abundance of cyanobacteria in addition to increases in other producer groups.

Subarctic cyanobacteria communities have undergone marked change. Cyanobacteria abundances have declined clearly in the Ba and the MBW zones indicating a decline of benthic communities. Cyanobacteria abundances have grown in the SPB zone and especially in sites, which have undergone browning or have been affected by human activity. Increased abundances of cyanobacteria in the southernmost sites can most probably be attributed to the increased abundance of planktic species. Environmental variables, responsible for the strongest impact on cyanobacteria abundances included TP, temperature and the amount of organic carbon.

Climate warming and browning are estimated to increase the abundances and bloom events of littoral benthic, and especially planktic cyanobacteria. In addition, toxin-producing species and harmful blooms are expected to increase. Climate warming is estimated to be a serious threat to the unique Arctic and subarctic benthic cyanobacteria-dominated aquatic ecosystems and these communities are predicted to be lost with irrevocable impacts to these ecosystems if climate warming is not mitigated.

Cyanobacteria species and community compositions in the subarctic need to be studied further in order to better understand and to be able to estimate the toxicological risks. Further study on the impact of lake browning on algal communities, and especially on cyanobacteria blooms, should be conducted. Lake ecosystem succession due to browning and climate warming should also be further studied in the subarctic to better understand vital warning signals, future trends and potential tipping points.

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Appendix 1. Limnological background information on 23 subarctic lakes. Kindly provided by Jan Weckström.

Lake number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
TP (µg/l)	L 2	3*	6	6	4	-	5	6	-	-	-	8	10	14	-	8	-	11	25	10	100	9	10
TN (µg/l)	110	97*	130	160	160	-	180	260	-	-	-	320	430	340	-	400	-	460	1200	240	350	280	360
TOC (mg/l)	1.11	1.83	2.70	2.17	2.23	8.90	3.24	7.29	4.90	6.50	4.80	5.96	9.48	7.26	4.20	7.14	7.20	8.52	8.23	8.91	9.07	8.34	8.57
Alkalinity (mmol/l)	0,00	0.16	0.11	4.27	3.66	8.50	3.66	6.10	9.00	9.50	9.50	4.27	0.61	10.98	4.00	4.27	4.50	0.61	1.22	6.10	9.76	0.00	2.44
Cond. (µS/cm)	5.90	27.70	18.20	11.60	12.80	37.70	13.30	23.90	28.00	33.50	32.80	11.90	13.50	29.30	6.40	9.40	16.00	5.20	6.40	17.20	18.70	7.20	10.69
pH	5.6	6.8	6.6	7.0	7.0	7.2	6.8	6.9	7.4	7.5	7.3	6.3	4.4	7.0	6.5	6.6	6.5	4.0	6.2	6.0	5.9	4.8	6.1
Bottom temp. (ºC)	7.3	4.6	8.2	13.4	12.0	-	10.2	15.0	-	-	-	17.0	16.8	8.6	-	16.6	-	17.9	16.4	4.2	11.0	16.8	16.7
Surface temp. July (ºC)	7.8	9.8	12.6	13.4	12.5	12.9	14.7	15.5	10.9	11.1	9.8	17.0	16.8	16.7	13.4	17.5	14.3	17.9	17.7	16.2	17.0	16.8	16.8
Sampling depth (m)	12.0	25.0	10.5	2.8	10.1	2.1	10.1	2.1	6.4	14.0	2.2	4.2	1.8	7.1	6.4	3.3	5.0	4.0	4.4	10.4	3.4	4.0	4.4
Max.depth (m)	12.0	29.5	10.5	2.8	10.1	2.1	10.1	2.1	6.4	17.0	2.9	4.2	1.9	7.1	6.4	4.1	5.0	4.3	4.4	10.4	3.4	4.0	4.0
LOI** (%)	13.5	20.5	19.6	34.0	33.61	55.0	54.5	48.3	38.2	35.7	38.2	60.4	80.8	42.3	49.4	58.6	61.2	83.6	88.0	42.3	50.1	71.8	64.1
Forest (zones)	Ba	Ba	Ba	Ba	Ba	MBW	MBW	MBW	MBW	MBW	MBW	BP	BP	BP	BP	BP	PB	PB	PB	PB	SPB	SPB	SPB
Mire area (%)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.93	0.00	0.33	0.00	25.75	58.82	22.68	1.50	2.38	0.00	0.00	4.45	12.03	45.95	28.81	40.03
Catch. Area (ha)	133.45	530.45	173.16	215.28	100.25	128.38	16.00	219.48	113.22	302.97	52.39	14.17	8.80	105.26	11.04	21.66	5.45	10.74	5.91	18.32	50.89	59.07	30.96
Area (ha)	9.61	69.86	16.89	20.44	9.33	3.85	3.47	6.05	13.91	10.27	1.39	2.55	1.97	28.18	2.58	2.18	0.90	1.33	1.52	4.01	4.34	10.67	7.14
Altitude (masl)	1009	679	687	774	796	526	596	463	526	498	508	322	332	319	317	313	263	253	252	249	249	262	268
Longitude (°E)	21.05	20.87	20.98	21.05	21.13	20.97	21.05	21.07	22.05	22.05	22.03	22.43	22.58	22.9	22.88	22.85	23.18	23.37	23.37	23.42	23.4	23.68	24.18
Latitude (°N)	69.17	69.05	69.05	69.06	69.03	68.92	68.92	68.9	68.68	68.67	68.67	68.47	68.42	68.42	68.40	68.4	68.20	68.13	68.12	68.1	68.01	67.98	67.85

Forest zones: SPB = spruce, pine and birch forest; PB = pine forest mixed with birch; BP = birch forest mixed with pine stands; MBW = mountain birch woodland; Ba = barren above the tree line